THE PHYLOGENETIC UTILITY OF LEMMATAL MICROMORPHOLOGY IN *LEPTOCHLOA* S.L. AND RELATED GENERA IN SUBTRIBE ELEUSININAE (POACEAE, CHLORIDOIDEAE, ERAGROSTIDEAE)[1]

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ABSTRACT

Micromorphological features of the lemma were investigated in the subtribe Eleusininae (Poaceae) using scanning electron microscopy. Ninety-two taxa were studied, which included 48 genera and all currently recognized species of *Leptochloa* s.l. All species of *Leptochloa* and a majority of genera in Eleusininae have cork cells, but silica cells are mostly absent in *Leptochloa* and most related genera in Eleusininae. Enneapogonoid-type microhairs are reported for *Cladoraphis cyperoides* and *Psammagrostis wiseana*, representing only the second report in Eleusininae. Although bicellular microhairs occur in most taxa, variations in microhair type, coupled with the occurrence of partitioning membranes, give them supra-specific phylogenetic utility. The occurrence of papillae on short and long cells varies within *Leptochloa* and between genera. Prickles are ubiquitous in *Leptochloa* and most related genera. Macrohairs are present in all species of *Leptochloa* but absent in some related genera. Clavicorniculate macrohairs are reported for one species each of *Leptochloa* and *Coelachyrum*, and a corniculate macrohair was observed in *Cynodon*. A crispate macrohair occurring in three species of *Coelachyrum* is described for the first time and probably represents a synapomorphy in that genus. The analysis of *Leptochloa* suggests that micromorphological characters vary little within a genus, and thus have the potential to serve as phylogenetic markers at the generic level. Uncertainty concerning the homologous relationships of papillae, hooks, prickles, and macrohairs is discussed in light of this study and previous literature.

RESUMEN

Las características micromorfológicas de la lema en la subtribu Eleusininae (Poaceae) se examinaron utilizando microscopía electrónica de barrido. Se estudiaron 92 taxa, 48 géneros, y todas las especies de *Leptochloa* hasta ahora reconocidas. Todas las especies de *Leptochloa* y la mayoría de los géneros de Eleusininae tienen células suberificadas, pero las células silicíferas están ausentes en *Leptochloa* y en la mayoría de los taxa de Eleusininae. Se reporta por segunda vez en Eleusininae la presencia de micropelos bicelulares de tipo enneapogonoid para *Cladoraphis cyperoides* y *Psammagrostis wiseana*. Aunque los micropelos bicelulares se presentan en casi todos los taxa, variaciones en el tipo de micropelo, junto con la presencia de membranas divisorias les dan valor diagnóstico para estudios filogenéticos supraespecíficos. La presencia de papilas de células cortas y estrechas es variable en *Leptochloa* y entre los otros géneros. Los aguijones se encuentran en todas las especies de *Leptochloa* y la mayoría de los géneros relacionados. Los macropelos están generalmente presentes en todas las especies de *Leptochloa* pero están ausentes en algunos taxa relacionados. Se reportan macropelos clavicorniculados para un especie de ambos géneros *Leptochloa* y *Coelachyrum*, y un macropelo corniculado se reporta para *Cynodon*. Un macropelo crispado en tres especies de *Coelachyrum* es descrito por primera vez, y quizá represente una sinapomorfía de cierto nivel en ese género. El análisis de *Leptochloa* indica que las características micromorfológicas varían poco, y por tanto tienen valor para estudios filogenéticos supraespecíficos. La dificultad sobre las relaciones homólogas de papilas, ganchos, aguijones, y macrotricomas se discute con base a lo hallado en este estudio y con datos anteriores de la literatura.

Cladistic estimations of phylogenetic history with morphological characters tend to favor the use of distinct qualitative characters, or those possessing easily defined character states. This tendency may reflect the potential pitfalls discussed by Chappill (1989) and Stevens (1991) in the uncritical use of

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quantitative characters (but see Thiele, 1993). Used alone, and due to the perception of high levels of homoplasy, characters of gross morphology have been considered inadequate as phylogenetic markers in the grass family (Thomasson, 1978; Hilu & Wright, 1982; Kellogg & Campbell, 1987; Davis & Soreng, 1993; Clark et al., 1995). Not surprisingly, revisionary studies of grasses are turning to micromorphological characters for additional phylogenetic data.

Epidermal micromorphological characters of grasses have systematic value between the ranks of subfamily and species (Prat, 1932; Tateoka et al., 1959; Metcalfe, 1960; Ellis, 1979). Descriptive studies of micromorphological features in grasses have focused on the surfaces of the leaf (Prat, 1932; summary in Ellis, 1976; see also Morden & Hatch, 1987; Dávila & Clark, 1990; Peterson & Annable, 1990; Barker, 1993; Scholz, 1993; Chen et al., 1993), glumes (Lucas, 1979; Molina, 1993), the lemma (Hsu, 1965; Thomasson, 1986; Peterson, 1989; Soderstrom & Zuloaga, 1989; Kellogg, 1990; Zuloaga & Judziewicz, 1991; Valdés-Reyna & Hatch, 1991; Naredo et al., 1993; Ball et al., 1993), and palea (summary in Consaul & Aiken, 1993: 1651). The phylogenetic application of micromorphological characters has been more limited (Peterson & Annable, 1992; Barker, 1993; Visser & Spies, 1994; Guala, 1995).

An Overview of Micromorphological Characters

Several categories of micromorphological characters have been recognized. Short cells (which include cork cells and silica cells), long cells, bicellular microhairs, papillae, hooks, prickles, and macrohairs are all examples of micromorphological characters (Metcalfe, 1960; Ellis, 1979). (See Ellis, 1979, for a summary of alternative terms for hooks and prickles.)

Short cells and long cells are readily distinguished on the basis of relative size, and (when both are present) may constitute a synapomorphy uniting Joinvilleaceae and Poaceae (see also Doyle et al., 1992; Kellogg & Linder, 1995). The differences between short cells and long cells have been documented thoroughly (Kaufman et al., 1969; Kaufman et al., 1970) and are evident in grass fossils of Miocene age (Thomasson, 1978, 1984). The elongation of long cells follows the initial differentiation of long cells and short cells (Kaufman et al., 1969; Kaufman et al., 1970). In addition to their extended length, long cells (unlike short cells) frequently have sinuous margins (Metcalfe, 1960; Clifford & Watson, 1977; Ellis, 1979; Chen et al., 1993). However, the distinction between long and short cells is not always absolute. Thomasson (1978: fig. 1d) illustrated long cells, identifiable by the sinuous margins, having similar dimensions to short cells for a fossilized species of the genus *Nassella* (tribe Stipeae). The two types of short cells recognized are cork cells (sometimes called suberin cells), which accumulate suberin (Kaufman et al., 1970), and silica cells, which accumulate silica into readily observed silica bodies.

Microhairs are bicellular structures that require high magnification for detection (Tateoka et al., 1959). (For exceptions to the bicellular condition see Dahlgren et al., 1985; Renvoize, 1985; and Zuloaga et al., 1989.) They are present throughout the family except in subfamily Pooideae (Johnston & Watson, 1976). Microhairs have been classified as "chloridoid," "panicoid," or "enneapogonoid," based on typological variants (Tateoka et al., 1959; Amarasinghe & Watson, 1988; Watson & Dallwitz, 1992). Only rarely is their ontological status as a distinct character uncertain. For example, as discussed by Barker (1993), the "long slender papillae" (Clayton & Renvoize, 1986: 165) common to several genera in Arundinoideae, given that they are reported to occasionally have the remains of a small apical cell (Renvoize, 1986: 328), may be interpretable as microhairs.

Papillae are short, undifferentiated processes that arise from the outer cell wall.

Hooks have been considered processes having a rounded base and an apex that is at least slightly pointed (Ellis, 1979), but are not recognized as a category in this study (see Discussion). Prickles are basally swollen processes having short, sharp apices that typically point toward the apex of the structure (leaves, glumes, lemmas, or paleas).

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Macrohairs are generally unicellular structures (but see Kabuye & Wood, 1969) visible to the naked eye.

Among lemmatal micromorphological structures, only microhairs have not been reported to accumulate silica. The presence of silica has been reported for cork cells (Kaufman et al., 1972); long cells (Ball et al., 1993); papillae (Terrell & Wergin, 1981; Consaul & Aiken, 1993); prickles (Soni et al., 1970; Kaufman et al., 1972 (as "trichomes"); Terrell & Wergin, 1981; Valdés-Reyna & Hatch, 1991; Ball et al., 1993); and macrohairs (Consaul & Aiken, 1993). (Stomata occasionally occur on lemmas. They are sufficiently infrequent in the taxa examined thus far to be considered an abnormal constituent of the lemma. In a study of the leaf of *Avena*, Kaufman et al. (1972) were unable to find silica in stomatal cells.)

Overview of Lemma Micromorphology

The lemma is the lower of two bracts that (usually) subtend each flower in grasses. The upper bract (the palea) is not homologous to the lemma (Clifford, 1987). The lemma is a transformational serial homology (de Pinna, 1991) of the leaf by virtue of its "ontogenetic individualization" (sensu Wagner, 1989a, b) from the leaf (Philipson, 1934; Tran, 1973; Kellogg, 1990). Its transformational derivation from the leaf is supported by rare atavisms in mutants to a leaflike progenitor having sheath, ligule, and blade (Philipson, 1934), its diminuitive size relative to regular leaves, its restricted occurrence in the inflorescence, the occasional presence of lemmatal stomata (common to the leaf), and the frequent infraspecific differences of micromorphological features between the leaf and lemma (Thomasson, 1978: 977; Terrell & Wergin, 1981: 706; Snow, unpublished).

The most extensive work on lemma micromorphology in Eleusininae was that of Valdés-Reyna and Hatch (1991). Their survey in Eragrostideae of 57 species (representing 30 genera) suggested such characters might be useful phylogenetic markers in the subtribe Eleusininae. This study extended their generic survey of micromorphology (Valdés-Reyna & Hatch, 1991) to include genera of Eleusininae not previously examined, including a few other genera in Chloridoideae, and to characterize these features for all species in *Leptochloa*.

An Overview of the Systematics of Chloridoideae

The grasses are composed of at least four monophyletic subfamilies and contain a number of tribes with uncertain phylogenetic affinity (Dahlgren et al., 1985; Kellogg & Campbell, 1987; Doyle et al., 1992; Davis & Soreng, 1993; Barker et al., 1995; Clark et al., 1995; Kellogg & Linder, 1995). The subfamily Chloridoideae Rouy has about 1300 species, which tend to occupy dry, warmer climates (Hartley & Slater, 1960). (Taxonomic concepts follow Clayton & Renvoize, 1986.) The largest tribe, Eragrostideae Stapf, has about 80 genera and 1000 species. Within Eragrostideae, the most diverse subtribe is Eleusininae Dumort, and only the highest latitudes are excluded from the overall range of its approximately 55 genera. Relatively few genera in Eleusininae occur outside of a single continent (e.g., *Coelachyrum, Eragrostis, Leptochloa, Trichoneura,* disregarding minor exceptions and a few cosmopolitan weeds). Excluding *Eragrostis*, with its approximately 350 species (Clayton & Renvoize, 1986; Van den Borre & Watson, 1994), most of the approximately 600 species in the subtribe occur in relatively small genera (10 species or fewer). *Leptochloa* P. Beauv. is a nearly worldwide genus of about 35 species, although many continue to segregate the genus *Diplachne* (McNeill, 1979; Phillips, 1982; Watson & Dallwitz, 1992; Simon, 1993; Nicora, 1995).

Recent intergeneric studies in Eleusininae differed in the taxa, characters, and analytical methodologies, which hampers meaningful comparisons between the results (Phillips, 1982; Hilu & Wright, 1982; Campbell, 1985; Hilu & Esen, 1993; Duvall et al., 1994). The position of *Leptochloa* in the generic arrangement of Clayton and Renvoize (1986: 192) suggests three non-mutually exclusive possibilities: (1) that *Leptochloa* has many close generic relatives, (2) that *Leptochloa* is evolutionarily basal to related genera, and (3) that *Leptochloa* may be paraphyletic as currently recognized. The monophyly of most chloridoid groups, including *Leptochloa,* remains largely untested.

The purpose of this paper is to create a more extensive data set for inferring phylogenetic relationships in *Leptochloa* and Chloridoideae (Snow, in prep.). In addition, terminological inconsistencies throughout the literature, coupled with the results herein, provide a basis to question the ontological status of several characters, and suggest the need for a critical reevaluation of the characters.

Material and Methods

The adaxial surface of the lemma was studied for 92 taxa using scanning electron microscopy (SEM) at the Electron Microscopy Laboratory at Washington University (Appendix 1). Samples were re-

moved directly from herbarium specimens. To assure the use of semaphorants (Wiley, 1981: 119), I generally sampled lemmas from spikelets that contained mature caryopses. This precaution was important, because spikelets in early stages of ontogeny may be present even when the inflorescence is well exserted from the leaf sheath. Three specimens of most taxa were observed. Some samples were sonicated in xylene for 30 minutes to remove the epicuticular waxes that can obscure surface features, but this treatment was not always effective. After being placed on aluminum stubs the specimens were coated with gold using a Polaron E5000 sputter coater. Samples were observed with 0° tilt at 20 kV on a Hitachi S-450 SEM and photographed using Polaroid 55 positive-negative film. Except for Figures 10 and 42, all photomicrographs have the apex of the lemma directed toward the right. Attempts to standardize the scale of photomicrographs proved unworkable, since various magnifications were necessary.

The format differs from Valdés-Reyna and Hatch (1991) in that microhairs and macrohairs are included, my interpretation of papillae on short cells is different (see Results), and the degree of undulation of the long cells with papillae was not recorded. Valdés-Reyna and Hatch (1991) discussed their findings based on four variations of cork cell occurrence: cork cells adjacent to silica cells; cork cells not adjacent to silica cells; cork cells papillate; or cork cells not observed. This study merely recorded cork cells as a binary character (present or absent). I will refer to taxa in Eleusininae besides *Leptochloa* as "Other Eleusininae Taxa" (OET), whereas other taxa in Eragrostideae (fide Clayton & Renvoize, 1986) will be designated "Other Eragrostoid Genera" (OERG).

This study focused on the presence or absence of characters. No attempt was made to measure quantitative variation of the characters, but distribution and frequency on the lemma is sometimes discussed.

Results

A summary of lemmatal microcharacters observed is presented in Table 1. For comparison, the results of Valdés-Reyna and Hatch (1991) are intercalated therein. Unless noted otherwise these results accord with those of Valdés-Reyna and Hatch (1991) for taxa examined in both studies. Figures are presented at the end of the text, arranged in alphabetical order by genus name. Figures are not presented for all taxa and characters observed or discussed, but virtually every character recorded (except those with question marks, Table 1) was verified with a photomicrograph.

Cork cells. Cork cells were abundant in the intercostal zones in all species of *Leptochloa,* and alternated with long cells. As was true of all micromorphological characters studied, their distribution could vary significantly on a single lemma. There was a general tendency for cork cells to decrease in frequency near the apex.

Among OET, cork cells were absent in *Desmostachya* (Fig. 14), *Ectrosia gulliveri* (Fig. 17), *Ectrosiopsis, Odyssea mucronata* (Fig. 60), and *Psammagrostis* (Fig. 65). Unlike its congener, *Odyssea paucinervis* has cork cells. The cork cells of *Apochiton* (Fig. 2), *Halopyrum* (Fig. 23), and *Neyraudia* (Fig. 58) were not noticeably darkened, as is common for mature cork cells under SEM observation (Valdés-Reyna & Hatch, 1991). However, since their size and location suggested cork cells, they were recorded as present (Table 1).

Cork cells were present in all OERG except *Spartina* (not shown). With the exception of a sparse distribution in *Tragus* (not shown), cork cells were common in OERG.

Some taxa had short cells resembling cork cells in size, and from which other structures could be seen developing, such as bicellular microhairs (e.g., *Bewsia,* Fig. 3), prickles (e.g., *Diplachne gigantea,* Fig. 38, *Leptochloa rupestris,* Fig. 48), and macrohairs (e.g., *Leptochloa fascicularis,* Fig. 36, *L. neesii,* Fig. 45). Many taxa such as *Eragrostiella* (Fig. 20) and *Indopoa* (Fig. 26) had short cells whose outer walls were rounded in profile, and which were ontogenetically destined to become cork cells. (Valdés-Reyna & Hatch (1991: 536) referred to these as papillate cork cells.) That they were destined to become cork cells became evident by examining different stages of development on a lemma, in which cells at the apical and basal portions were in different stages of development. The initially rounded outer walls of short cells appear to collapse coincident with or prior to suberin deposition; this process was evident in the shrunken tissue of the outer wall, coupled with darkened lumens of the short cells (e.g., *Leptocarydion,* Fig. 28, *Leptochloa uniflora,* Fig. 51, and *L. virgata,* Fig. 52).

Silica cells. Silica cells were absent in all species of *Leptochloa* except for *L. monticola* (Fig. 41), which had abundant silica cells in all specimens examined, and one specimen (*Snow 5811-A*) of *L. fascicularis* (Fig. 35), which had a few silica cells present in the intercostal regions.

A majority of OET genera had silica cells. In *Halopyrum* (Fig. 23, not visible) they were poorly developed (minimal silica deposition?), obscured

Table 1. Summary of lemmatal micromorphological characters for species of *Leptochloa*, most genera in Eleusininae, and a few genera in Eragrostideae outside Eleusininae (fide Clayton & Renvoize, 1986). Genera not included in Eleusininae are indicated with a double asterisk. Taxa are arranged alphabetically. Taxa examined by Valdés-Reyna and Hatch (1991) but not examined herein are followed by single asterisk; their data are intercalated for convenience by: (1) relying on Watson and Dallwitz (1992) for the type of microhair (as they determined from leaf blades); (2) examining herbarium material for the presence of prickles and macrohairs (Appendix 1); and (3) by leaving a question mark in the column for papillate short cells, since their interpretation of papillae differed (see Results). The generic abbreviation for species tentatively placed in *Leptochloa* that apparently lack a valid combination in the latter is *D.* (for *Diplachne*) + specific epithet. Abbreviations: + = present; − = absent; BM = bicellular microhairs (C = chloridoid, P = panicoid, E = enneapogonoid); Macrohairs (N = normal, CC = clavicorniculate, A = apiculate, CR = crispate); PLC = papillate long cells; PSC = papillate short cells.

Taxon	Cork	Silica	BM	PLC	PSC	Prickles	Macrohairs
Acrachne racemosa	+	−	C	−	−	+	−
Apochiton burttii	+	−	C	−	−	+	N
Bewsia biflora	+	−	C	−	−	+	N
*Bouteloua curtipendula***	+	−	C	−	−	+	N
Brachychloa schiemanniana	+	−	C	−	−	+	−
*Chloris paniculata***	+	−	C	−	−	+	N
*Chloris verticillata***	+	−	C	−	−	+	N
Cladoraphis cyperoides	+	+	E	−	−	+	N
Cladoraphis spinosa	+	+	−	−	−	+	−
Coelachyrum brevifolium	+	−	C	−	−	+	CR
Coelachyrum poiflorum	+	−	C	−	−	+	CR
Coelachyrum stoloniferum	+	−	C	−	−	+	CR
Coelachyrum yemenicum	+	−	C	−	−	+	CC
*Chondrosum gracile***	+	−	C	−	−	+	N
*Cynodon nlemfuensis***	+	−	C	−	−	+	A/N
*Dactyloctenium**	+	−	C	−	?	−	−
Desmostachya bipinnata	−	+	C/P	−	−	+	−
Dinebra polycarpha	+	−	C	+	+	+	N
Dinebra retroflexa	+	−	C	+	+	+	N
Drake-Brockmania haareri	+	−	C	+	+	+	N
Drake-Brockmania somalensis	+	−	C	+	+	+	N
Ectrosia gulliveri	−	+	P	−	−	+	N
Ectrosia leporina	+	+	P	−	−	+	−
Ectrosiopsis lasioclada	−	+	P	−	−	+	−
Eleusine indica	+	+	C	−	−	+	−
Eragrostiella bifaria	+	−	C	−	−	−	−
Eragrostis spp. *	+	+	C/P	−	?	+	−
Erioneuron spp.*	+	+	C	−	?	+	N
Gouinia virgata	+	−	C	−	−	+	N
Habrochloa bullockii	+	−	P	−	−	+	N
Halopyrum mucronatum	+	+	C	+	+	+	N
Harpachne schimperi	+	+	C	−	−	+	±
Heterachne abortiva	+	+	P	−	−	+	−
Indopoa paupercula	+	−	C	−	−	+	N
Kengia serotina	+	+	C	+	−	+	N
Leptocarydion vulpiastrum	+	+	C	−	−	+	N
Leptochloa aquatica	+	−	C	−	−	+	N
D. caudata	+	−	C	−	−	+	N
Leptochloa chinensis	+	−	C	+	−	+	N
Leptochloa chloridiformis	+	−	C	−	−	+	N
Leptochloa ciliolata	+	−	−	−	−	+	N
Leptochloa coerulescens	+	−	C	+	−	+	N
D. cuspidata	+	−	−	+	−	+	N
Leptochloa decipiens	+	−	−	−	−	+	N
Leptochloa digitata	+	−	C	−	−	+	N
Leptochloa divaricatissima	+	−	C	−	−	+	N

Table 1. Continued.

Taxon	Cork	Silica	BM	PLC	PSC	Prickles	Macrohairs
Leptochloa dubia	+	−	C	−	−	+	N
D. eleusine	+	−	C	−	−	+	CC
Leptochloa fascicularis	+	±	C	+	+	+	N
Leptochloa fusca	+	−	C	+	+	+	N
D. gigantea	+	−	C	+	+	+	N/−
Leptochloa ligulata	+	−	C	−	−	+	N
Leptochloa longa	+	−	C	−	−	+	N
Leptochloa marquisensis	+	−	C	−	−	+	N
Leptochloa monticola	+	+	C	−	−	+	N
Leptochloa mucronata	+	−	C	−	−	+	N
D. muelleri	+	−	C	+	+	+	N
Leptochloa nealleyi	+	−	C	−	−	+	N
Leptochloa neesii	+	−	C	−	−	+	N
Leptochloa obtusiflora	+	−	C	−	−	+	N
Leptochloa panicea	+	−	C	+	−	+	N
Leptochloa panicoides	+	−	C	+	+	+	N
D. parviflora	+	−	C	+	−	+	N
Leptochloa rupestris	+	−	C	−	−	+	N
Leptochloa scabra	+	−	C	−	−	+	N
Leptochloa sp. nov. (Snow, in prep.)	+	−	C	−	−	+	N
Leptochloa squarrosa	+	−	C	+	−	+	N
Leptochloa uniflora	+	−	C	−	−	+	N
Leptochloa uninervia	+	−	C	+	+	+	N
Leptochloa virgata	+	−	C	−	−	+	N
Leptochloa viscida	+	−	C	+	+	+	N
Leptochloa xerophila	+	−	C	−	−	+	N
*Lintonia nutans***	+	−	C	−	−	+	N
Lophacme digitata	+	−	C/P	−	−	+	N
*Munroa squarrosa**	−	−	C	+	?	+	N
Myriostachya wightiana	+	+	C	−	−	+	−
Neesiochloa barbata	+	−	C	−	−	+	N
Neyraudia reynauldiana	+	−	P	−	−	+	N
Ochthochloa compressa	+	−	C	−	−	+	N
Odyssea mucronata	−	+	C	+	−	+	N
Odyssea paucinervis	+	+	C	+	−	+	N
Orinus thoroldii	+	−	C	+	+	+	N
Oropetium aristatum	−	−	C	+	−	+	N
Pogonarthria fleckii	+	+	C	−	−	+	N
Pogoneura biflora	+	+	C	−	−	+	N
Psammagrostis wiseana	−	+	E	−	−	+	−
Psilolemma jaegeri	+	+	C	−	−	−	−
*Redfieldia flexuosa**	−	−	C	−	?	+	−
Richardsiella eruciformis	+	+	C	−	−	+	N
Sclerodactylon macrostachyum	+	+	C	−	−	+	−
*Scleropogon brevifolius**	+	+	C	+	?	+	N
*Sohnsia filifolia**	+	+	C	−	?	−	−
*Spartina pectinata***	−	+	C	−	−	+	N
Steirachne barbata	+	+	C	−	−	+	−
*Tragus pedunculatus***	+	+	C	+	+	+	N
Trichoneura grandiglumis	+	−	C	−	−	+	N
Tridens spp.*	+	−	C	−	?	+	N
Triplasis spp.*	+	−	C	−	?	±	N
Tripogon major	+	−	C	−	−	+	N
Triraphis andropogonoides	+	+	P	−	−	+	N
*Vaseyochloa multinervosa**	+	−	C	−	?	+	N
Viguierella madagascariensis	+	+	−	−	−	+	−

by epicuticular waxes, or both. *Kengia* (Fig. 27, not visible) and *Eleusine* (not illustrated) had a few silica cells that were localized over the costal zones. The proximity of silica cells to cork cells was a character noted by Valdés-Reyna and Hatch (1991). Silica cells were not adjacent to cork cells in *Desmostachya* (Fig. 14), *Ectrosia gulliveri* (Fig. 17), *Ectrosiopsis* (Fig. 19), *Myriostachya* (Fig. 56), *Odyssea mucronata* (Fig. 60), and *Steirachne* (Fig. 69). Silica cells were adjacent to cork cells in *Cladoraphis* (Fig. 7), *Ectrosia leporina* (Fig. 18), *Harpachne* (Fig. 24), *Odyssea paucinervis* (not shown), *Psilolemma* (Fig. 66), *Richardsiella* (Fig. 67), and *Sclerodactylon* (Fig. 68). In *Pogonarthria* (Fig. 63) and *Triraphis* (Fig. 71) their location varied (cork cells adjacent to silica cells not shown for *Triraphis*). It was uncertain whether the dark, narrow bands adjacent to some silica cells in *Heterachne* (Fig. 25) were artifacts of preparation (e.g., shrinking of cell walls adjacent to the silica bodies noted by Kaufman et al., 1972: fig. 6, and Terrell & Wergin, 1981) or whether the narrow bands were cork cells that were partially obscured by overarching silica bodies; the uncertainty was enhanced because not all silica cells had adjacent bands. Since a few short cells with dark lumina were visible adjacent to some silica cells, cork cells were scored as present for *Heterachne*. I did not observe silica cells on *Leptocarydion*, but given their observation by Valdés-Reyna and Hatch (1991: fig. 24, tab. 2), they were recorded as present (Table 1).

Among OERG, silica cells were observed in *Spartina* and *Tragus*, being more common in the latter.

Bicellular microhairs. Chloridoid microhairs were observed in all species of *Leptochloa* except *L. ciliolata*, *Diplachne cuspidata*, and *L. decipiens*. Microhairs generally were scattered, but in *Leptochloa caudata* and *L. longa* they were common near the apex. The basal cells of microhairs of *Leptochloa panicoides* (Fig. 47) and *L. viscida* (Fig. 53) were atypically thick and nontapering toward their basal insertion. Additional study is needed to evaluate whether the shape of the basal cell can be hypothesized as a separate character.

Among OET, seven eleusinioid genera had panicoid microhairs (*Ectrosia gullivieri*, *Habrochloa*, *Heterachne*, *Neyraudia*, *Steirachne*, *Triraphis*, *Viguierella*), whereas the remaining OET had chloridoid microhairs. Microhairs were not observed in *Cladoraphis spinosa* or *Viguierella*, the latter of which needs further study, since only one specimen was available for study (Table 1). As with species of *Leptochloa*, microhairs varied in abundance and were generally scattered; only near the apex in *Apochiton* and *Triraphis* were they common. Nicora (1962: 9) illustrated enneapogonoid microhairs in Eleusininae for *Neeragrostis*, which Clayton and Renvoize (1986) included in *Eragrostis*. The enneapogonoid microhairs observed here for *Cladoraphis cyperoides* and *Psammagrostis wiseana* (Fig. 65) represent only the second report for this type in Eleusininae. All microhairs in *Psammagrostis* (Fig. 65) had swellings distal to the base of the microhair, a condition not observed elsewhere.

All OERG had chloridoid microhairs.

Papillae. Papillae occurred singly on short cells or singly on the distal ends of long cells. Three clarifications are needed prior to presenting observations of papillae.

First, the distal ends of the outer walls of epidermal *long* cells can be noticeably swollen, as in *Eragrostiella* (Fig. 20), *Indopoa* (Fig. 26), and *Leptochloa virgata* (Fig. 52). These swellings were recognized by Valdés-Reyna and Hatch (1991: fig. 23) in at least one instance as papillae. As I interpret them, outer walls that are merely swollen are distinct from true papillae. The distinction between long cells possessing a single, distal papilla (e.g., *Leptochloa coerulescens*, Fig. 31) and long cells that are merely swollen can be seen with *Leptochloa chinensis* (Fig. 29), in which a single papilla is evident atop the distal swelling of a long cell, and with *L. fusca* (Fig. 37), in which long cells are either papillate or merely swollen. Second, the outer wall of *short* cells prior to differentiation can appear rounded (papillate, fide Valdés-Reyna & Hatch, 1991) when viewed in profile (e.g., *Eragrostiella*, Fig. 20; *Indopoa*, Fig. 26). The rounded outer walls should not be confused with papillae, which are localized processes arising from the outer wall. Third, the apical extensions of the lateral walls of long cells of *Leptocarydion* (Fig. 28) and *Steirachne* (Fig. 69) are distinct from true papillae; Palmer and Gerbeth-Jones (1988: 94) have noticed a similar distinction in *Phacelurus* (Panicoideae, Andropogoneae), as did Peterson (1989) in *Muhlenbergia* (Chloridoideae, Sporobolinae). Thus, for this study papillae are taken to be apically rounded, undifferentiated processes that arise from and are localized on the outer cell wall, and which can become silicified (Clark & Gould, 1975; Terrell & Wergin, 1981; Consaul & Aiken, 1993). (Ellis (1979) cited Metcalfe (1960) that papillae can become cutinized. However, Metcalfe (1960: 668) indicated only one species (*Trikeraia hookeri* (tribe Stipeae)) as having cutinized papillae. Furthermore, Metcalfe (1960) did not indicate how he determined the presence of cutin.) It is important to stress that other structures on grasses called papillae may not be

homologous to the papillae described here (Clark & Gould, 1975; Zuloaga, 1987: fig. 26.2c; Dávila & Clark, 1990; Filgueiras et al., 1993; Jenks et al., 1994).

Papillae on short cells. Papillae on short cells occurred in several species of *Leptochloa* (*L. fascicularis, L. fusca, Diplachne gigantea, D. muelleri, L. panicoides, L. uninervia,* and *L. viscida*). In most cases they had a collapsed appearance, which may have been an artifact of preparation, or, since the silicification of papillae has been documented (Clark & Gould, 1975; Terrell & Wergin, 1981; Consaul & Aiken, 1993), perhaps was an indication that silica deposition had not occurred. Collapsed papillae on short cells are frequent in the literature (e.g., Palmer & Gerbeth-Jones, 1986: pl. 15a–f).

Relatively few OET had papillae on short cells (*Dinebra* spp.; *Drake-Brockmania* spp., Fig. 16; *Halopyrum,* Fig. 23; *Orinus,* Fig. 61). Only in *Halopyrum* (Fig. 23) were the papillae large. Unlike Valdés-Reyna and Hatch (1991) I did not detect papillae on short cells of *Eleusine* (not shown).

Among OERG, only *Tragus* (not shown) had papillae on the short cells.

Papillae on long cells. In the 13 species of *Leptochloa* having a single papilla on the long cells (Table 1) the papillae were more frequently present near the apex of the lemma. *Leptochloa fusca* (Fig. 37) and *Diplachne parviflora* (not shown) were inconsistent in this feature even over localized portions of the lemma; some long cells had papillae, others did not. *Leptochloa viscida* (Fig. 53) had only a few papillae near the lateral veins. The size of the papillae arising on long cells was more or less constant within *Leptochloa,* with the exception of *L. coerulescens* (Fig. 31), in which the papillae were noticeably longer. In some cases the papillae were weakly developed, as in *Diplachne cuspidata* (not shown) and *Diplachne gigantea* (Fig. 38).

Although many OET had long cells with swollen ends (e.g., *Bewsia,* Fig. 3; *Coelachyrum yemenicum,* Fig. 12; *Trichoneura,* Fig. 70, in part; compare with *Coelachyrum poiflorum,* Fig. 10, in which the long cells have no swellings), relatively few had a single papilla on the long cells (*Dinebra,* Fig. 15; *Drake-Brockmania,* Fig. 16; *Kengia,* Fig. 27; *Odyssea,* Fig. 60, not visible; *Orinus,* Fig. 61; and *Oropetium,* Fig. 62). The significantly greater basal diameter of papillae in *Halopyrum* differs from other taxa in Eleusininae.

Long cells with papillae were absent in the OERG.

Prickles. Prickles were observed in every species of *Leptochloa* and tended to increase in frequency toward the apex. Among *Leptochloa* species prickles were rare in *Diplachne cuspidata, L. digitata, L. mucronata, L. rupestris, L. uniflora,* occasional in most species, or common, as in *L. caudata.*

Prickles were observed for all OET. A single prickle was observed on *Psilolemma*; however, since only one was observed on three specimens, and because its apex was directed toward the lemmatal base (almost universally they point toward the apex in Eleusininae), it was considered an abnormality and recorded as absent. Prickles were most abundant in *Cladoraphis* spp. (Figs. 6, 7), *Ectrosia* spp. (Figs. 17, 18), *Gouinia* (Fig. 21), *Halopyrum* (Fig. 23), and *Oropetium* (Fig. 62). Unlike Valdés-Réyna and Hatch (1991), prickles were observed (with a dissecting microscope) on herbarium specimens of *Tridens* spp., *Vaseyochloa multinervosa,* and *Triplasis purpurea,* although they were occasionally only infrequently present at the apex.

Prickles occurred on all OERG. *Spartina* (not shown) had prickles of widely different sizes. Prickles were generally most abundant on the awns of species bearing these structures (e.g., *Lintonia,* Fig. 54); in *Pogoneura,* prickles were restricted to the awn.

Macrohairs. All species of *Leptochloa* had at least some macrohairs on the lemmas. They were not observed using SEM on *Diplachne gigantea,* but analysis of an isotype (*Vesey-Fitzgerald 1551*; BM) with a dissecting microscope revealed the presence of short macrohairs along the edges of the midrib of some lemmas. In some species they are rare, such as the sparse basal occurrence on *Leptochloa digitata* (Fig. 32). Most macrohairs observed in *Leptochloa* were typical in having smooth edges and a rounded or acute tip. However, a "clavicorniculate" type (see Discussion) was found in *D. eleusine,* in which the subapical portion was noticeably clavate, and above which occurred a corniculate tip. This feature was noted earlier by Phillips (1974, 1982) for *D. eleusine, Coelachyrum yemenicum, Lintonia,* and *Trichoneura.* The hairs shown for *Tribolium obliterum* by Visser and Spies (1994: fig. 3b) may be clavicorniculate, but this is uncertain since only their apices are shown.

A majority of OET had macrohairs on the lemma; they were absent in *Acrachne* (Fig. 1), *Cladoraphis spinosa* (Fig. 7), *Desmostachya* (Fig. 14), *Ectrosia leporina* (Fig. 18), *Ectrosiopsis* (Fig. 19), *Eleusine* (not shown), *Eragrostiella* (Fig. 20), *Heterachne* (Fig. 25), *Myriostachya* (Fig. 56), *Psilolemma* (Fig. 66), *Sclerodactylon* (Fig. 68), *Steirachne* (Fig. 69), and *Viguierella* (Fig. 72). Only two macrohairs were observed at the very base of one specimen (*Faden et al. 74/613,* Appendix 1) of *Harpachne schimperi.*

The study of several herbarium sheets at MO revealed that a few macrohairs occasionally occur on the edges near the base of some lemmas. However, they are at most infrequent and are always relatively short. Moreover, given their length, one could just as easily designate them as (relatively long) prickles. Examination of specimens of *H. bogdanii* (MO: *Heady 1466*, *Bogdan 4524*), the other species in the genus, also revealed a few short hairs near the base of some lemmas. Given their sporadic occurrence and their questionable status as hairs (vs. relatively long prickles), I have recorded them as present or absent (Table 1). The abundant macrohairs on *Apochiton* (Fig. 2) made observation of other features difficult. The clavicorniculate hairs of *Coelachyrum yemenicum* appear identical to those of *Diplachne eleusine*. A crispate macrohair, identifiable by the irregular ("crisped") surface and apparently reported here for the first time in grasses (Uphof, 1962; Metcalfe, 1960; Ellis 1976, 1979), was observed for *Coelachyrum brevifolium* (Fig. 8), *C. poiflorum* (Figs. 9, 10), and *C. stoloniferum* (Fig. 11). The crisping is expressed most thoroughly toward the apex, and somewhat less so basally. Some macrohairs of *Trichoneura grandiglumis* (Fig. 70) were swollen at the base.

Among the OERG surveyed, only *Spartina* lacked macrohairs. Some specimens of *Cynodon nlemfuensis* (Fig. 13) had macrohairs with distinctly "apiculate" (sensu Peterson, 1989) tips.

Discussion

This study originated from morphologically based cladistic studies of *Leptochloa* using various combinations of likely sister genera, as hypothesized by Clayton and Renvoize (1986). The sole use of gross morphology gave poorly resolved consensus trees and clades with low support values (Snow, unpublished). Moreover, the use of a single data set may have resulted in artificial groupings, a potential problem Hilu and Wright (1982) alluded to in their phenetic study of chloridoid grasses. These factors suggested that additional characters might lead to more "accurate" (sensu Hillis & Bull, 1993) estimations of the phylogenetic relationships. Given that micromorphological characters have known systematic value in grasses (references in Introduction), this study was undertaken to enlarge extant data sets for purposes of phylogenetic inference.

Cork Cells. Given their universality in *Leptochloa*, cork cells are of no phylogenetic value in the genus.

However, the variable presence of cork cells in Eleusininae and Eragrostideae suggests they are phylogenetically informative at the generic level. Cork cells were recorded as present only when the short cell was substantially darkened (as viewed by SEM), whereas Palmer and associates generally recorded cork cells as present when any undifferentiated short cell occurred adjacent to a silica cell (e.g., Palmer et al., 1985: pl. 1e, 2e, 3e, 4c, and many others therein). I agree with J. T. Columbus (pers. comm., January 1995) that the extent to which suberin deposition actually occurs, and the extent to which it can be observed, needs further investigation. If suberin deposition in short cells is eventually demonstrated to be invisible to SEM, or it is shown that "cork cells" on lemmas are lacking in suberin, then their use as phylogenetic markers will need reconsideration. These considerations aside, I have followed others (e.g., Valdés-Reyna & Hatch, 1991) by recording cork cells as either present or absent.

Silica Cells. Lemmatal silica cells were mostly absent from *Leptochloa*, and thus have minimal infrageneric phylogenetic value. Since only one specimen of *L. fascicularis* (Fig. 35) had a few silica cells, their occurrence on that specimen is probably similar to lemmatal stomata, which occasionally reappear as atavisms from the transformationally antecedent leaves. However, in *Leptochloa monticola* (Fig. 41) silica cells are common, which requires a reassessment of earlier research. Using several lines of evidence, Valls (1978) suggested that *L. monticola* was generically misplaced. Based on leaf anatomy and citing Clifford and Watson (1977), Valls (1978) suggested a possible alliance with *Chionochloa* Zotov (Arundinoideae, Arundineae). To assess a possible alliance with Arundineae, I sampled lemmas from *Chionochloa conspicua* (Forst. f.) Zotov subsp. *cunninghamii* (Hook. f.) Zotov, *C. flavescens* Zotov, *Danthonia dominguensis* Hack. & Pilg., and *Rytidosperma pilosum* (R. Br.) Connor & Edgar (Appendix 1; data not shown). Unlike *L. monticola*, which had chloridoid microhairs, the microhairs of *C. conspicua* var. *cunninghamii* and *R. pilosum* were panicoid; furthermore, microhairs were not seen for *C. flavescens* or *D. dominguensis*. Of relevant note, Watson and Dallwitz (1992) reported panicoid microhairs (for the abaxial leaf surface) for *Danthonia*, which does not accord with the chloridoid microhairs of *Leptochloa monticola*. In addition, the species of *Chionochloa* lacked cork cells, which were present in *L. monticola*. Morever, the dumbbell-shaped silica bodies in *L. monticola* differed from the saddle-shaped silica bodies of *C. flavescens* and *D. dominguensis*. Whereas each of these taxa has at least one discrepancy when compared to *L. monticola*, lemmatal

micromorphology alone does not support an obvious relationship of *L. monticola* to Arundineae.

Saddle-shaped (Clifford & Watson, 1977; Valls, 1978), dumbbell-shaped (Valls, 1978), and cross-shaped (Metcalfe, 1960) silica bodies have been reported for leaf blades in *Leptochloa*. Valls (1978: 82) has shown that both dumbell-shaped and saddle-shaped silica bodies occur in *Leptochloa dubia*. Ovate and saddle-shaped silica bodies were observed for *Odyssea mucronata*. The presence of two shapes of silica bodies on *L. dubia* and *O. mucronata* cautions against their uncritical use as diagnostic or phylogenetic markers. Recognition of shape differences of silica bodies as distinct characters (or character states) thus seems premature until it can be demonstrated that infraspecific variation in silica body shape is minimal. This caveat is supported by studies in *Oryza* (Whang & Kim, 1994) and *Zizania* (Terrell & Wergin, 1981) (both genera in tribe Oryzeae), which documented extensive infraspecific variation in the shape of silica bodies.

Ignoring for the moment silica body shape, and focusing on mere presence or absence, silica cells appear to be important phylogenetic markers, since they were not observed in over half of the OET and OERG examined. Their presence on the lemma is probably symplesiomorphic, given the near universal occurrence of silica bodies in grass leaves, and that the lemma is transformationally homologous to the leaf. Testing for parallel loss or gain, however, will require a cladistic approach (Snow, in prep.).

Bicellular microhairs. The lack of microhairs (e.g., *Leptochloa ciliolata, Diplachne cuspidata, L. decipiens*) is not unequivocal evidence for their absence, since a single microhair was often all that was visible for three or more specimens of a given taxon. Microhairs were not restricted to certain portions of the lemma, but, when infrequent, were usually found near the apex. In some taxa, such as *Lintonia*, they extend onto the awn. Given a simple presence or absence, microhairs probably would be of little phylogenetic value in Eleusininae. However, two features of microhairs suggest their utility as systematic markers. First, Amarasinghe and Watson (1988) demonstrated that ten chloridoid genera, including *Leptochloa*, have partitioning membranes in the basal cell of the microhair. Moreover, the membranes were limited to the subfamily Chloridoideae (Amarasinghe & Watson, 1988: 307). Of the genera they surveyed in Eleusininae, *Eragrostis, Pogonarthria,* and *Triraphis* lacked the membranes. The use of partitioning membranes as a potential phylogenetic marker in the subfamily merits further investigation over a wider range of taxa. Second, with few exceptions (e.g., *Eragrostis,* Watson & Dallwitz, 1992), microhairs can be readily assigned to one of three morphological types: chloridoid, panicoid, or enneapogonoid, based on morphological differences of the basal and distal cells and their length ratios (Tateoka et al., 1959; Jacobs, 1987; Amasaringhe & Watson, 1988; Watson & Dallwitz, 1992; but see below also).

The elongated aspect and thin wall of the distal cells in the microhairs of seven OET (e.g., *Habrochloa,* Fig. 22) characterize them as panicoid microhairs (Table 1), which in all cases accords with the observations of Watson and Dallwitz (1992) for leaves.

The discovery of enneapogonoid microhairs on the lemmas of *Cladoraphis cyperoides* and *Psammagrostis wiseana* represents the third report of enneapogonoid microhairs outside the tribe Pappophoreae (Chloridoideae) and the second in Eleusininae. They were first reported for *Amphipogon strictus* (Arundinoideae) by Amarasinghe and Watson (1988). Earlier, Watson and Dallwitz (1992: 232) were unable to find microhairs on leaf blades of *C. cyperoides* from photographic material provided by R. P. Ellis. Of the bicellular microhairs illustrated by Tateoka et al. (1959), the microhair of *C. cyperoides* seems to most resemble those of *Sporobolus vaginiflorus* (Tateoka et al., 1959: fig. b,64) and *Pappophorum elegans* (Tateoka et al., 1959: fig. b,155). It also somewhat resembles a microhair reported by Peterson (1989: fig. 2,d) for two species of *Muhlenbergia.* The swelling distal to the base of the microhairs in *Psammagrostis* (Fig. 65) was absent elsewhere in Eleusininae.

Although not identified as such, an enneapogonoid microhair was recently shown for the arundinoid species *Pentameris distichophylla* (Barker, 1993: fig. 1,c). The recognition of three morphological categories of microhairs admittedly represents typological thinking, which can misguide the understanding of biological reality (Mayr, 1982). Thus, when making preliminary hypotheses of homology (de Pinna, 1991), one might consider whether the "enneapogonoid" microhairs of *Cladoraphis cyperoides* and *Psammagrostis wiseana* are homologous with those occurring in *Enneapogon,* or whether the relative elongation of the basal cell is a "character" itself, the elongation having been achieved independently from the enneapogonoid type. Overall, the distinct morphologies of microhairs in Eleusininae and their tendency to be restricted generically together suggest their potential value as indicators of phylogenetic relationships.

Papillae. The characterization and interpretation of papillae were initially confounded by several

factors (see Results). Despite the more restricted criteria given above, the presence or absence of papillae is probably of phylogenetic value in *Leptochloa* and other genera in Eleusininae. The papillae on short cells were almost always collapsed, and thus could be confused with the collapsing outer wall of short cells, which apparently occurs during suberin deposition of cork cells (see above). That these structures could rightly be called papillae only suggested itself after repeated comparisons between numerous photos of taxa with and without this feature, and seeing similar photos of collapsed papillae in the literature. The papillae on short cells are perhaps best revealed on *Drake-Brockmania somalensis* (Fig. 16).

All members of the *Leptochloa fusca* group (tentatively: *Diplachne cuspidata*, *L. fascicularis*, *L. fusca*, *Diplachne gigantea*, *D. muelleri*, *D. parviflora*, *L. uninervia*) have a single papilla located distally on long cells, as well as having some short cells with a single papilla. Other characters that suggest a close relationship among its members include an apically attenuated ligule, relatively long spikelets, spikelets with frequently five or more florets, the perisperm of the caryopsis being only weakly adnate to the endosperm, and a pronounced lacuna in the midvein of the leaf blade (Snow, in prep.). *Leptochloa chinensis* and *L. coerulescens*, which both have papillae on long cells, have not been previously hypothesized to be closely related. Many species of *Leptochloa* have never been apportioned into subgenera or sections, but based on Clayton and Renvoize (1986), papillate species that would be placed in section *Diplachne* include the *L. fusca* group, *L. panicoides*, and *L. viscida*, whereas other papillate species would be placed in section *Leptochloa*. Papillae on short cells are also known from *Festuca* (Consaul & Aiken, 1993) and other genera in Pooideae (Thomasson, 1986).

Of the Eleusininae genera studied herein reported to have papillae (Valdés-Reyna & Hatch, 1991), I observed them only in some species of *Leptochloa*. This is due to the different interpretation of papillae used for this analysis (Results). The papillae of *Halopyrum*, which have a larger basal diameter than related genera, approximate a condition found in some genera of other subfamilies (e.g., *Brachiaria* (Panicoideae, Paniceae), Zuloaga & Soderstrom, 1985; fig. 2d; *Olyra* (Bambusoideae, Olyreae), Soderstrom & Zuloaga, 1989; fig. 21c), in which the entire outer wall swells outward, thus making more difficult the distinction between papillae and swollen outer walls.

Among OERG, I was unable to determine whether *Tragus* had papillae on short cells, since distinguishing between long and short cells was difficult; this uncertainty is reflected by the question mark in Table 1.

Prickles. Whereas Valdés-Reyna and Hatch (1991) did not observe prickles in their sample of *Leptochloa*, I found a universal occurrence of prickles in the genus. Given their universality and assuming that *Leptochloa* is monophyletic, they have no phylogenetic value. Others have suggested that the location of micromorphological characters (e.g., costal vs. intercostal zones) should be noted (Ellis, 1979; Consaul & Aiken, 1993). However, no obvious differences in costal and intercostal zones were noted for *Leptochloa*. Peterson (1989) differentiated between regular prickles and apiculate prickles in some species of *Muhlenbergia*, but this distinction did not hold in *Leptochloa*, OET, and OERG (but see comments below under macrohairs).

The phylogenetic value of prickles is similar for OET, since only *Psilolemma* was lacking this character. Species of *Trichoneura* and *Tripogon* studied by Valdés-Reyna and Hatch (1991) lacked prickles, but I observed them in other species of these genera (Table 1). As documented so thoroughly by Dávila and Clark (1990) for leaf blade epidermal micromorphology, all species need to be sampled to fully assess the occurrence of prickles and other micromorphological features within a genus.

That the size of prickles could vary on a lemma is most evident in *Spartina* (not shown), in which prickles on the margin of the lemma dwarfed those in the intercostal zones. Sizable differences were also evident in *Apochiton*, *Cladoraphis spinosa*, *Dinebra retroflexa* (Fig. 15), *Leptochloa longa*, *L. nealleyi* (Fig. 44), and *L. scabra*. Others have found discrepancies in lemmatal or laminar prickles within a species (Prat, 1948: his large and small "spicules"; Davies, 1959: his "asperities" and "incipient asperities"; Ball et al., 1993: compare fig. 1 with fig. 8; Thomasson, 1986: fig. 15, and note the increasing size of prickles between figs. 2, 5, and 7; Barker, 1993: fig. 2a–d).

In several cases prickles were flat at the base or had weak conduplicate basal folding (present but not shown in: *Orinus*, *Leptochloa fascicularis*, *L. monticola*, *Diplachne muelleri*), a condition illustrated (Zuloaga, 1987: fig. 26.4d; Thomasson, 1986: figs. 4, 17; Valdés-Reyna & Hatch, 1991: fig. 44) and discussed (Consaul & Aiken, 1993: 1656) earlier for other taxa. The conduplicate condition may be an early expression of prickle ontogeny in which the outer wall evaginates prior to its expansion, after which silica deposition may occur and the rigidity of the prickle is achieved. The accumulation of silica in the tips of prickles (Consaul & Aiken,

1993) probably explains their brittleness and propensity to break (e.g., *Gouinia, Kengia* (Fig. 27)).

Two categories of prickles (prickles and hooks) have historically been recognized (Metcalfe, 1960; Ellis, 1979). The tendency to distinguish between hooks and prickles reflects the frequent occurrence on specimens of two distinct sizes of projections of the outer wall (e.g., Palmer & Gerbeth-Jones, 1986: pl. 10a,c & pl. 12c,f; Dávila & Clark, 1990: fig. 34). Since the distinction between them seems absolutely arbitrary *within Eleusininae* (e.g., note gradations in *Dinebra retroflexa*, Fig. 15), I have chosen not to recognize hooks. Metcalfe (1960) suggested that hooks were homologous with prickles. His use of the term homology was probably invoking the concept of intermediate forms (Remane, 1952; Sattler, 1984), which illustrates their common developmental trajectories, and which according to some intepretations of homology (de Queiroz, 1985) establishes their homology. Ellis (1979: 668) indicated that prickles on leaf blades originate from short cells, but prickles clearly also arise from long cells of lemmas on *Gouinia* (Fig. 21), *Kengia, Leptochloa monticola* (Fig. 41), *Lintonia* (Fig. 54), and *Pogonarthria* (Fig. 63). If prickles continue to be recognized as characters distinct from macrohairs (but see below), it will be necessary to recognize that prickles can arise from either short cells (Ellis, 1979) or long cells (this study).

Macrohairs. Ellis (1979) has stated that macrohairs arise from long cells. Kellogg (1990: 1983) noted that the arachnose lemmatal hairs of *Poa* appear to initiate from short cells, but only because those cells have not yet elongated into long cells. My observations indicate that macrohairs can arise from long cells or short cells. Their origin from short cells is most evident in *Bewsia* (Fig. 3), *Leptochloa fasicularis* (Fig. 36), *L. neesii* (Fig. 45), and *Neesiochloa* (Fig. 57). On long cells, they can arise from the proximal end, as is evident in *Coelachyrum yemenicum* (Fig. 12), *Diplachne eleusine* (Fig. 34), *Trichoneura* (Fig. 70), *Triraphis* (Fig. 71), or rarely on the distal end, as for example in *L. mucronata* (Fig. 42).

In *Leptochloa* spp., normal macrohairs were generally restricted to the lower and middle portions of the nerves. A clavicorniculate type was observed for *Diplachne eleusine* (Fig. 34), which was also present in *Coelachyrum yemenicum* (Fig. 12). Phillips recognized clavicorniculate hairs for both *D. eleusine* and *Coelachyrum yemenicum* (as *Cypholephis yemenica*), calling them "club-shaped" (Phillips, 1974) and later "clavate" (Phillips, 1982: 155). Since the hairs have a distinctly narrowed portion above the subapical swelling, the clavicorniculate designation seems to best describe their morphology. (The assistance of D. Nicolson in matters of terminology is here acknowledged.) Clayton and Renvoize (1986) distinguished *Leptochloa* from *Coelachyrum* in part by the broadly elliptic, concavo-convex, rugulose caryopsis of the latter. The inflorescence of *Diplachne eleusine* resembles that of *C. yemenicum* in having few, relatively short, and more or less erect spicate branches. In addition, the caryopsis characters of the two species are similar in outline and cross-sectional shape, and in having a smooth pericarp that is weakly adnate to the endosperm (Snow, unpublished). Like most species of *Leptochloa* and unlike most species of *Coelachyrum*, the grain of *C. yemenicum* is not rugulose. Watson and Dallwitz (1992) segregated *C. yemenicum* into the monotypic genus *Cypholepis* and mentioned the presence of clavicorniculate hairs. Phylogenetic studies are needed to determine the generic affinites of *D. eleusine* and *C. yemenicum*, but the above evidence, along with cladistic studies by Van den Borre (1994: 216), suggests they may be phylogenetically close.

This study is the first to document the crispate macrohair, which occurs in *Coelachyrum breviflorum* (Fig. 8), *C. poiflorum* (Figs. 9, 10), and *C. stoloniferum* (Fig. 11). It is characterized by an irregular wrinkling (crisping) of the surface, which is expressed most fully toward the apex. That the wrinkling was found repeatedly in these taxa and not elsewhere suggests it was not an artifact of preparation. In grasses, the morphological "type" most resembling the crispate type is that of *Danthoniopsis viridis* (Panicoideae, Arundinelleae), which has a sparsely papillate shaft (Palmer & Tucker, 1981: fig. 9f). It differs from the crispate type in that significant portions of the shaft are relatively smooth. Infrequent and irregular papillate bulges on the shaft of macrohairs have been noted sporadically on the lemmas of *Neostapfia colusana* Davy and *Orcuttia pilosa* Hoover (Snow, unpublished), both members of the tribe Orcuttieae (Chloridoideae). Trichomes having micropapillate wall sculpturing were reviewed by Uphof (1962) and recently have been noted in Rubiaceae (Sullivan, 1986) and Verbenaceae (Rueda, 1994). The exclusive occurrence of crispate macrohairs in three species of *Coelachyrum* suggests it is a synapomorphy at some level in that genus.

As mentioned above, Peterson (1989) used the term "apiculate" to distinguish between the apices of prickles in some species of *Muhlenbergia*. This distinction is useful for the apices of some macrohairs. The apices of macrohairs in two specimens (*Crook 2115, Gereau et al. 3490*) of *Cynodon nlem-*

fuensis (Fig. 13) were noticeably apiculate in comparison to other taxa (Appendix 1). The possible systematic significance of apiculate tips warrants further attention.

Peterson (1989) also recognized "swollen base" macrohairs in some species of *Muhlenbergia*. Some, but not all, macrohairs of *Trichoneura grandiglumis* (Fig. 70) had this feature. Macrohairs with swollen bases may arise from long cells, which have a larger foundation relative to short cells. Future research should evaluate whether macrohairs have normal or swollen bases.

It is important to distinguish between the base of the macrohair and the surrounding cells that can swell outward to buttress the macrohair at its base (Ellis, 1979: 657). Swollen cells adjacent to lemmatal macrohairs have been called (collectively) tubercles or papillate bases, and were noted in OET only for *Richardsiella* (Fig. 67) and in OERG for *Tragus* (not shown). The tubercles were much larger in *Richardsiella*.

Like prickles, the basal portion of some macrohairs was distinctly flattened or somewhat conduplicate, as in *Bewsia* (Fig. 3), *Chloris verticillata* (Fig. 5), *Coelachyrum yemenicum* (Fig. 12), *Leptochloa neesii* (Fig. 45), and *L. squarrosa* (Fig. 50). This condition is evident in some macrohairs of the unrelated genus *Olyra* (Soderstrom & Zuloaga, 1989: fig. 6c). Ontogenetic stages of macrohair elongation can be seen with three closely spaced hairs on *Chloris verticillata* (Fig. 5). As with prickles, the outer wall of the cell appears to evaginate in a conduplicate manner and flatten as the macrohair begins development. Although most fully developed macrohairs lack the folded base, the base sometimes remains flattened (*Coelachyrum yemenicum*, Fig. 12; *Leptochloa neesii*, Fig. 45; *L. squarrosa*, Fig. 50; and *Neesiochloa*, Fig. 57). The base of macrohairs can be hollow, as evidenced by basally severed hairs in *Leptochloa fusca* (Fig. 37) and *Ochthochloa* (Fig. 59).

Phylogenetic utility of lemmatal micromorphology. Micromorphological characters generally vary little in *Leptochloa*. With few exceptions, cork cells were present, silica cells were absent, chloridoid bicellular microhairs were present, prickles were present, and macrohairs were present. The occurrence of papillae on long cells and short cells was more variable, suggesting their presence or absence may be phylogenetically informative within the genus.

In addition to *Leptochloa*, seven genera were studied for two or more species. Overall, little intrageneric variation was generally observed for given characters. For example, only *Odyssea* varied in its expression of cork cells (Table 1). As so thoroughly documented by Dávila and Clark (1990) for the leaf blades of *Sorghastrum*, a complete survey of all species is necessary to fully characterize a genus. So, although further study is needed, it appears that lemmatal micromorphological characters within genera of Eleusininae are largely conservative. However, as evident from Table 1, significant variation occurred between genera. As such, micromorphological characters are probably reliable phylogenetic markers at the generic level.

Micromorphological characters and problems of homology. The micromorphological characters in this study have been reported and discussed following the tradition of Metcalfe (1960) and Ellis (1979). That is, cork cells, silica cells, bicellular microhairs, papillae, prickles, and macrohairs have been treated separately, without questions having been raised about their ontological status as distinct characters. However, abundant evidence from the literature suggests that papillae, hooks, prickles, and macrohairs often represent arbitrary stages along one or two developmental trajectories. (If we recognize the fundamental difference between long and short cells, and if we therefore choose to differentiate between the outward extensions of the outer cell walls of short cells vs. long cells (into papillae, hooks, prickles, macrohairs), then one might argue that there are separate developmental trajectories for outer cell wall extensions of short and long cells.)

Confounding matters has been an inconsistency in the previous use of terminology. As one of many examples, the cupulate papillae in *Muhlenbergia* (subfamily Chloridoideae; Peterson, 1989) resemble the hooks of some *Melica* spp. (subfamily Pooideae; Thomasson, 1986). This may simply reflect differences in papillae at the subfamilial level, or suggest that papillae between the two subfamilies are not homologous. As a second example, most agrostologists have seen the gradual transition that occurs in the axils of the primary branches on the rachis from "prickles" to "macrohairs." Such transitions are easily found on individual specimens. Statements such as

> . . . it seems probable that those [prickles] that eventually become pointed may pass through an unbarbed phase [i.e., papillae and/or hooks] during their ontogenetic development, but this possibility needs further investigation (Metcalfe 1960: xxiv)

and

> The distinction between macrohairs and prickles is often not clear . . . (Ellis 1979: 667)

suggest that the distinction between character and

character state is ambiguous, and illustrate the need for reconsidering the relationship between homology and ontogeny for these features.

Morden (1985: 36), upon examination of micromorphological characters on the lemma and palea of some species of *Muhlenbergia*, stated "The presence of papillae on the epidermis of the floret appears to represent the initiation of villous [i.e., macrohair] growth, whether or not elongation follows." The photomicrographs (Morden, 1985: figs. 12–19, 24–27) reveal that the papillae on immature florets (lemmas and paleas) are present in regions where macrohairs develop on mature florets. The thinning of epicuticular waxes on the elongating papillae (Morden, 1985: fig. 25) suggests that wax-covered papillae can elongate into macrohairs (given, it is assumed, some sort of genetic signal). However, since some grasses can have several papillae per cell (Metcalfe, 1960; Ellis, 1979), it is doubtful that all papillae represent early stages in the ontogeny of macrohairs.

To be used as phylogenetic markers, there must be no ambiguity surrounding the ontological status of characters. Regarding papillae, hooks, prickles, and macrohairs, it remains necessary to question which entitites can be meaningfully compared as homologous characters (Haszprunar, 1992), since gradations between "characters" can be seen on *individual* specimens: e.g., (1) between papillae and hooks (Thomasson, 1986: figs. 1, 4, 7, 12, 14); (2) between papillae and prickles (Dávila & Clark, 1990: fig. 29); (3) between papillae and macrohairs (Morden, 1985; discussed above); (4) between hooks and prickles (Thomasson, 1986: figs. 4, 15; Dávila & Clark, 1990: fig. 3); and (5) between prickles and macrohairs (Palmer & Gerbeth-Jones, 1988: pls. 9c, 10a, 28f; Valdés-Reyna & Hatch, 1991: fig. 36; Consaul & Aiken, 1993: fig. 23; Barker, 1993: fig. 2b). Given these observations, the distinctions between papillae, hooks, prickles, and macrohairs have been somewhat arbitrary at best.

Although the uncertain homology status of several micromorphological characters and their questionable value as phylogenetic markers should now be evident, it would be premature to assert that distinctions between them are always arbitrary, and that they thus hold no phylogenetic value. Rather, previous research and the results herein indicate the need for a thorough review of the ontological status of papillae, hooks, prickles, and macrohairs. If these features are not ontogenetically individualized structures that are comparable across taxic hierarchies, then their utility as phylogenetic markers is suspect. Their phylogenetic application needs to be evaluated in light of theoretical considerations of ontogeny and homology (e.g., Patterson, 1982; Roth, 1984, 1991; de Queiroz, 1985; Wagner, 1989a, b; de Pinna, 1991; Hall 1992, 1994) and will be the basis of a subsequent paper (Snow, in prep.).

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Appendix 1. Species, authorities, collectors, and country of origin of specimens studied. Order of taxa is alphabetical. Not all taxa are in subfamily Chloridoideae (see Discussion). Taxa scattered within *Leptochloa* with the generic abbreviation "*D.*" (for *Diplachne*) lack a valid combination in *Leptochloa*. All vouchers at MO unless an herbarium acronym follows the country of origin. Identifications of specimens were verified using: Bor, 1973; Clayton, 1972; Clayton et al., 1974; Cope, 1985a, b; Elffers & Kennedy-O'Byrne, 1957; Gibbs Russell et al., 1990; Gould, 1975; Judziewicz, 1990; McVaugh, 1983; Ortíz, 1993; Simon, 1993; Tsvelev, 1976; Tutin, 1980.

Acrachne racemosa (Roem. & Schult.) Owhi: *De Wilde 6876*, Ethiopia; *Patel & Kaunda 4259*, Malawi; *Crook 837*, Zambia. *Apochiton burttii* C. E. Hubb.: *Braun 226*, Tanzania; *Sabaya 83*, Tanzania; *Greenway & Kanuri 14445*, Tanzania.

Bewsia biflora (Hack.) Gooss.: *Strid 2911*, Zambia; *Davidse 5968*, South Africa; *Wild 1685*, Zimbabwe. *Bouteloua curtipendula* (Michx.) Torr.: *Palmer 31445*, U.S.A.; *Thomas 107107*, U.S.A.; *Goodding 2463*, U.S.A. *Brachychloa schiemanniana* (Schweick.) S. M. Phillips: *Balsinhas 1129*, Mozambique; *Elffers s.n.*, Mozambique (US).

Chloris paniculata Scribn.: *Stewart 260*; Cocos Island (Costa Rica). *Chloris verticillata* Nutt.: *Snow 5779*, U.S.A.; *Henderson 69-307*, U.S.A.; *Gould 7804*, U.S.A. *Chondrosum gracile* Kunth: *Beetle & Guzman M-5579*, Mexico; *García 6*, Mexico; *Thieret & Brandenburg 53242*, U.S.A. *Chionochloa conspicua* (Forst. f.) Zotov subsp. *cunninghamii* (Hook. f.) Zotov: *Gardner 3307*, New Zealand. *Chionochloa flavescens* Zotov: *Mason 2920*, New Zealand. *Cladoraphis cyperoides* (Thunb.) S. M. Phillips (85): *Davidse 33370*, South Africa; *Lavranos & Pehlemann 19640*, Namibia; *Goldblatt 4244*, South Africa. *Cladoraphis spinosa* (L. f.) S. M. Phillips: *Davidse 33301*, South Africa; *Bayliss 5732*, South Africa; *Davidse 33265*, South Africa. *Coelachyrum brevifolium* Hochst.: *Adam 21799-4*, Mauritania; *Dwyer 13928a*, Saudi Arabia. *Coelachyrum poiflorum* Chiov.: *De Wilde & De Wilde-Duyfjes 10617*, Ethiopia; *De Wilde & De Wilde-Duyfjes 7975*, Ethiopia; *Boulos & Getahun 11906*, Ethiopia. *Coelachyrum stoloniferum* C. E. Hubb.: *Wieland & Gahair 4010*, Somalia; *Wieland 4098*, Somalia. *Coelachyrum yemenicum* (Schweinf.) S. M. Phillips: *Ellis 2643*, Botswana; *Gilbert & Gilbert 2335*, Ethiopia; *Leistner 1315*, South Africa. *Cynodon nlemfuensis* Vanderyst: (89) *Gereau et al. 3490*, Tanzania; *Grant s.n.*, Kenya; *Crook 2115*, Zimbabwe.

Danthonia dominguensis Hack. & Pilg.: *Zanoni et al. 37703*, Dominican Republic. *Desmostachya bipinnata* (L.) Stapf: *Fosberg 56909*, Pakistan; *Matamir 7/8*, Egypt; *Dwyer 13120*, Saudi Arabia. *Dinebra polycarpha* S. M. Phillips: *Ndegwa 639*, Kenya. *Dinebra retroflexa* (Vahl) Panz.: *Tanner 1430*, Tanzania; *Faden & Faden 74/741*, Kenya; *Schimper 1610*, Ethiopia. *Drake-Brockmania haareri* (Stapf & C. E. Hubb.) S. M. Phillips: *Mbano 5753*, Tanzania; *Drummond & Hemsley 2287*, Tanzania; *Bogdan 5434*, Kenya (US). *Drake-Brockmania somalensis* Stapf: *Heady 1815*, Kenya; *Faden & Faden 74/991*, Kenya; *Robertson 1755*, Kenya.

Ectrosia gulliveri F. Muell.: *Lazarides 4745*, Australia; *Blake 13574*, Australia. *Ectrosia leporina* R. Br.: *Clarkson 4892*, Australia; *Blake 18655*, Australia; *Clarkson 6059*, Australia. *Ectrosiopsis lasioclada* (Merr.) Jansen: *Lazarides 4787*, Australia. *Eleusine indica* (L.) Gaertn.: *Snow 5777*, U.S.A.; *Irwin et al. 11276*, Brazil; *Auquier 2142*, Zaire. *Eragrostiella bifaria* (Vahl) Bor: *Davidse & Sumithraarachchi 8991*, Sri Lanka; *Ash 648*, Ethiopia; *Faden & Faden 74/967*, Kenya.

Gouinia virgata (J. Presl) Scribn.: *Stevens & Moreno 18445*, Nicaragua; *Ventura 9239*, Mexico; *Seymour 3305*, Nicaragua.

Habrochloa bullockii C. E. Hubb.: *Webster T234*, Tanzania. *Halopyrum mucronatum* (L.) Stapf: *Ash 708-A*, Ethiopia; *Davidse & Sumithraarachchi 8224*, Sri Lanka; *Wingfield 4396*, Tanzania. *Harpachne schimperi* A. Rich.: *Davidse 9224*, Kenya; *Faden et al. 74/613*, Kenya; *Amshoff 6468*, Ethiopia. *Heterachne abortiva* (R. Br.) Hughs: *Must 1213*, Australia; *Clarkson 3700*, Australia; *Lazarides 9250*, Australia.

Indopoa paupercula (Stapf) Bor: *Santapau 10287*, India; *Santapau 10269*, India; *Saldanha 17978*, India.

Kengia serotina (L.) Packer: *Suza 655*, Czech Republic; *Svestka s.n. (MO 1743346)*, Czech Republic; *Clemens 1616*, China.

Leptocarydion vulpiastrum (De Not.) Stapf: *Ndegwa 655*, Kenya; *Crook 818*, Zimbabwe; *Van Jaarsveld 412*, South Africa. *Leptochloa aquatica* Scribn. & Merr.: *Hitchcock 674*, Mexico; *Arsène 5760-A*, Mexico. *D. caudata* K. Schum.: *Lewys Lloyd 1*, Tanzania; *Kingollah 39*, Kenya. *L. chinensis* (L.) Nees: *Yao Kan et al. 79280*, Japan (China?); *Hsu 1392*, Taiwan; *Davidse & Sumithraarachchi 9006*, Sri Lanka. *L. chloridiformis* (Hack. ex Stuck.) Parodi: *Pensiero & Vegetti 2752*, Argentina; *Venturi 5724*, Argentina. *L. ciliolata* (Jedwabn.) S. T. Blake: *Anderson 738*, Australia; *Blake 5860*, Australia; *Hubbard 3217*, Australia. *L. coerulescens* Steud.: *Adam 14030*, Senegal; *Adam 17175*, Senegal; *Adam 27799*, Liberia. *D. cuspidata* Launert: *Giess & van dor Wait 12632*, Namibia. *L. decipiens* (R. Br.) Stapf ex Maiden: *Blake 12707*, Australia. *L. dig-*

itata (R. Br.) Domin: *Chippendale & Constable 19009*, Australia; *Clemens 21*, Australia; *Lazarides 3797*, Australia. *L. divaricatissima* S. T. Blake: *Blake 10517*, Australia; *Johnson 410*, Australia; *Blake 19152*, Australia. *L. dubia* (Kunth) Nees: *Snow 5857*, U.S.A.; *Pringle 1027*, Mexico; *Renvoize & Cope 4240*, Bolivia; *Stuckert 17257*, Argentina. *D. eleusine* Nees: *Maguire 8398*, South Africa; *Giess 8422*, Namibia; *Brown & Shapiro 166*, South Africa. *L. fascicularis* (Lam.) A. Gray: *Snow 5811-A*, U.S.A.; *Davidse et al. 11647*, Brazil; *Wingfield 5867*, Venezuela. *L. fusca* (L.) P. Beauv. ex Roemer & Schult.: *Davidse & Sumithraarachchi 9174*, Sri Lanka; *Leippert 4606*, Namibia; *Davidse & Sumithraarachchi 9119*, Sri Lanka; *Clemens 1615*, China; *Hubbard & Winders 6405*, Australia. *D. gigantea* Launert: *Smith 1387*, Botswana. *L. ligulata* Lazarides: *Jacobsen E58*, Australia (BRI); *Thompson & Sharpe CHA293*, Australia (BRI); *Anderson 704*, Australia (BRI). *L. longa* Griseb.: *Croat 16903*, Panama; *Hitchcock 672*, Trinidad; *Davidse 2612*, Trinidad. *L. marquisensis* (F. Br.) P. M. Peterson & Judz.: *Wagner & Lorence 6222*, Marquesas; *Lorence et al. 6230*, Marquesas; *Perlman 10242*, Marquesas. *L. monticola* Chase: *Leonard 4751*, Haiti (B); *Ekman 3075*, Haiti (US); *Ekman 1576*, Haiti (US). *L. mucronata* (Michx.) Kunth: *Snow 5801-A*, U.S.A.; *Raveill 1813*, U.S.A.; *McKenzie 1160*, U.S.A. *D. muelleri* Benth.: *Lazarides 5329*, Australia. *L. nealleyi* Vasey: *Snow 5814*, U.S.A.; *Swallen 10267*, U.S.A.; *Thomas & Allen 123786*, U.S.A. *L. neesii* (Thwaites) Benth.: *Davidse & Sumithraarachchi 9180*, Sri Lanka; *Davidse 7466*, Sri Lanka; *Wirawan 657*, Sri Lanka. *L. obtusiflora* Hochst.: *Mhoro 1868*, Tanzania; *De Wilde 6449*, Ethiopia; *Verdcourt 1101*, Kenya. *L. panicea* (Retz.) Owhi: *McGusker 229*, Tanzania; *Reekmans 8750*, Burundi. *L. panicoides* (J. Presl) Hitchc.: *Snow 5790*, U.S.A.; *Summers & Hudson 4596*, U.S.A.; *Nelson et al. 3213*, Honduras. *D. parviflora* (R. Br.) Benth.: *Lazarides 4400*, Australia. *L. rupestris* C. E. Hubb.: *Wood 2848*, Yemen (BM); *Pappi 2960*, Eritrea (US). *L. scabra* Nees: *Snow 5795-A*, U.S.A.; *Pohl & Davidse 12062*, Honduras; *Davidse 2617*, Trinidad. *L.* sp. nov. (Snow, in prep.): *Davidse & Sumithraarachchi 9066*, Sri Lanka. *L. squarrosa* Pilg.: *Mwasumbi & Mponda 12671*, Tanzania; *Bond 144*, Tanzania; *Greenway 5096*, Tanzania. *L. uniflora* Hochst. ex A. Rich.: *Davidse & Ellis 5925*, South Africa; *Greenway et al. 14075*, Tanzania; *Ellis 2780*, Zimbabwe. *L. uninervia* (J. Presl) Hitchc. & Chase: *Snow 5789*, U.S.A.; *McDaniel & Rimachi 23074*, Peru; *Garcia & Quevedo s.n.*, Puerto Rico. *L. virgata* (L.) P. Beauv.: *Snow & Evans 4392-C*, U.S.A.; *Ramírez 1687*, Venezuela; *Irwin et al. 11332*, Brazil. *L. viscida* (Scribn.) Beal: *Snow 5817*, U.S.A.; *Thurber 45*, U.S.A.; *Wright 2044*, U.S.A. *L. xerophila* P. M. Peterson & Judz.: *Decker 637*, Marquesas. *Lintonia nutans* Stapf: *Faden & Faden 74-747*, Kenya; *Ndegwa 599*, Kenya; *Ngoni 319*, Botswana. *Lophacme digitata* Stapf: *Smook 1453*, South Africa; *Anderson 36*, South Africa.

Myriostachya wightiana (Nees ex Steud.) Hook. f.: *Davidse & Sumithraarachchi 9027*, Sri Lanka; *Davidse & Sumithraarachchi 9051*, Sri Lanka; *Griffith 6621*, India.

Neesiochloa barbata (Nees) Pilg.: *Harley et al. 16293*, Brazil; *Boyle 347*, Brazil; *Irwin et al. 31661*, Brazil. *Neyraudia reynauldiana* (Kunth) Kena ex Hitchc.: *Liu 890113*, China; *Levine 1812*, China; *Maxwell 86-218*, Thailand.

Ochthochloa compressa (Forssk.) Hilu: *Dwyer 13928*, Saudi Arabia; *Munro s.n.* (MO 2964652), India; *Stewart 1387*, India. *Odyssea mucronata* (Forssk.) Stapf: *Ash 708*, Ethiopia. *O. paucinervis* (Nees) Stapf: *Leydu 703*, Namibia; *Leistner 2262*, South Africa; *Ellis 2767*, South Africa. *Orinus thoroldii* (Stapf) Bor: *Younghusband 147*, Khamajong. *Oropetium aristatum* (Stapf) Pilg.: *Fay 5932*, Central African Republic; *Adam 31611*, French Guinea; *Adam 14998*, Sudan.

Pogonarthria fleckii (Hack.) Hack.: *Rodin 9073*, Namibia; *Goldblatt 1901*, Namibia; *Giess 11285*, Namibia. *Pogoneura biflora* Napper: *Greenway & Turner 10608*, Tanzania (PRE); *Greenway et al. 10620*, Tanzania (US). *Psammagrostis wiseana* C. A. Gardner & C. E. Hubbard: *J. Stretch s.n.*, Australia (CANB). *Psilolemma jaegeri* (Pilg.) S. M. Phillips: *Greenway 10288*, Tanzania; *Greenway & Kanuri 13530*, Tanzania; *Bullock s.n.* (MO accession 1819125), Tanzania.

Richardsiella eruciformis Elffers & Kenn.-O'Byrne: *Phipps & Vesey-Fitzgerald 3227*, Zambia; *Webster A340*, Zambia (two sheets at MO; I sampled accession 2324532). *Rytidosperma pilosum* (R. Br.) Connor & Edgar: *Gardner 1372*, New Zealand.

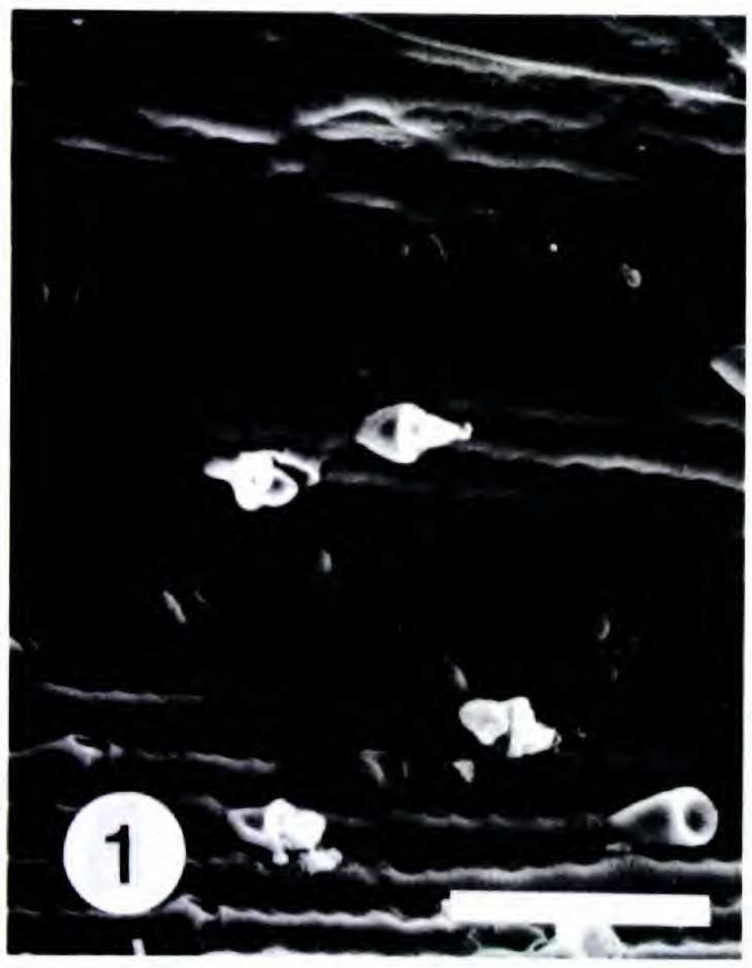
Sclerodactylon macrostachyum (Benth.) A. Camus: *Croat 30943*, Madagascar; *Fosberg 48752*, Aldabra Island (West Island). *Spartina pectinata* Link: *Hayden 11*, U.S.A.; *Conrad 10063*, U.S.A.; *Johnston 509*, U.S.A. *Steirachne barbata* (Trin.) Renvoize: *Stergios et al. 9733*, Venezuela; *Cuello 756*, Venezuela; *Maas & Westra 3771*, Guyana.

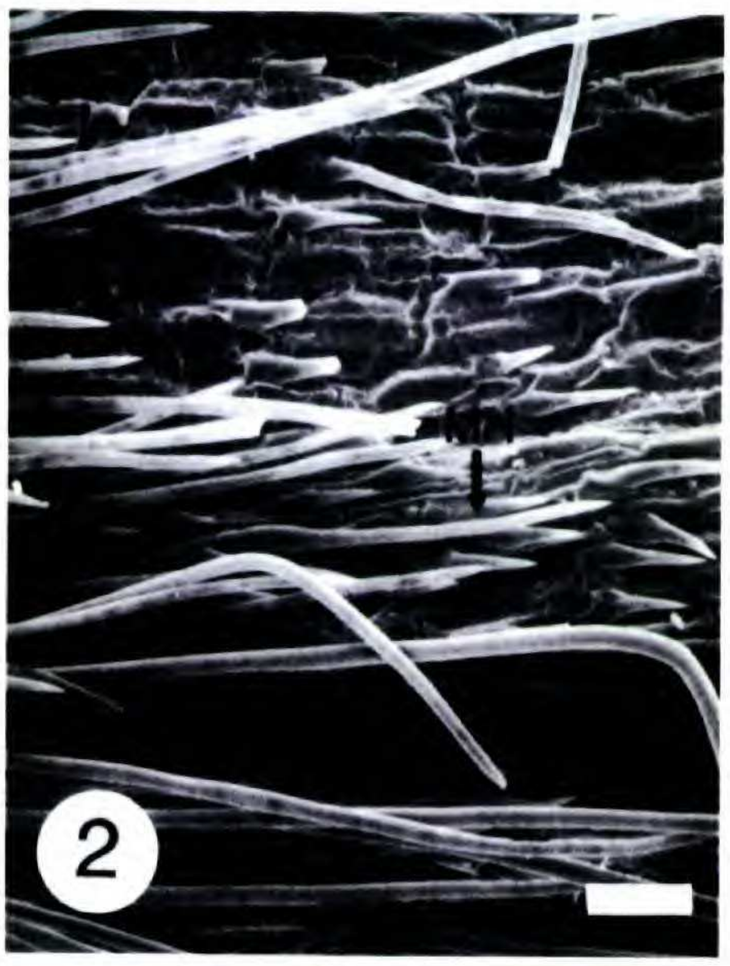
Tragus pedunculatus Pilg.: *Dinter 5698*, South Africa; *Ellis 2700*, South Africa. *Trichoneura grandiglumis* (Nees) Stapf & C. E. Hubb.: *Biegel 733*, Zimbabwe; *Ferreira F168*, South Africa; *Brain 1242*, Zimbabwe. *Tripogon major* Hook. f.: *Jacques-Georges 22087*, Sierra Leone; *Bogdan 3932*, Kenya; *Thulin & Mhoro 3040*, Tanzania. *Triraphis andropogonoides* (Steud.) E. Phillips: *Smook & Gibbs-Russell 2192*, South Africa; *Smook 3008*, South Africa; *Scheepers 1313*, South Africa.

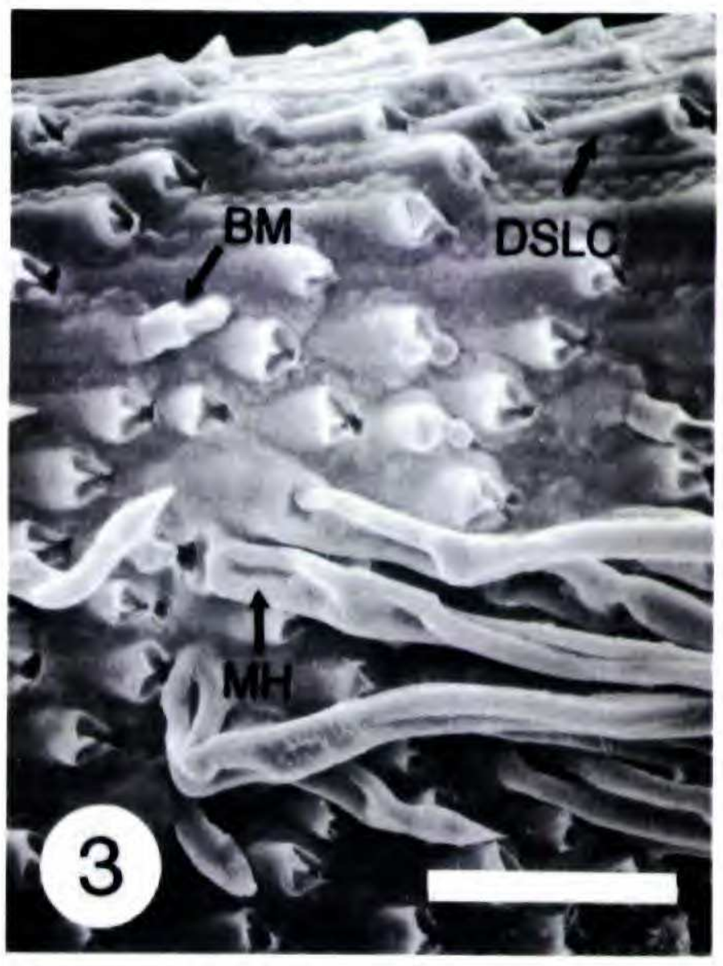
Viguierella madagascariensis A. Camus: *Gentry 11882*, Madagascar.

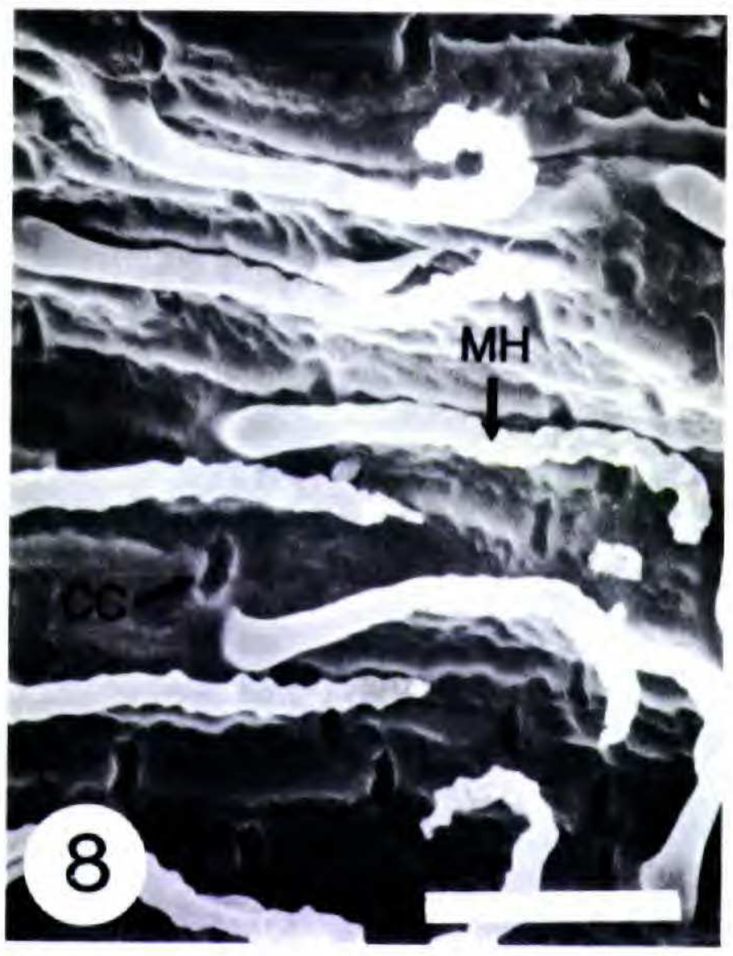
Note added in proof.

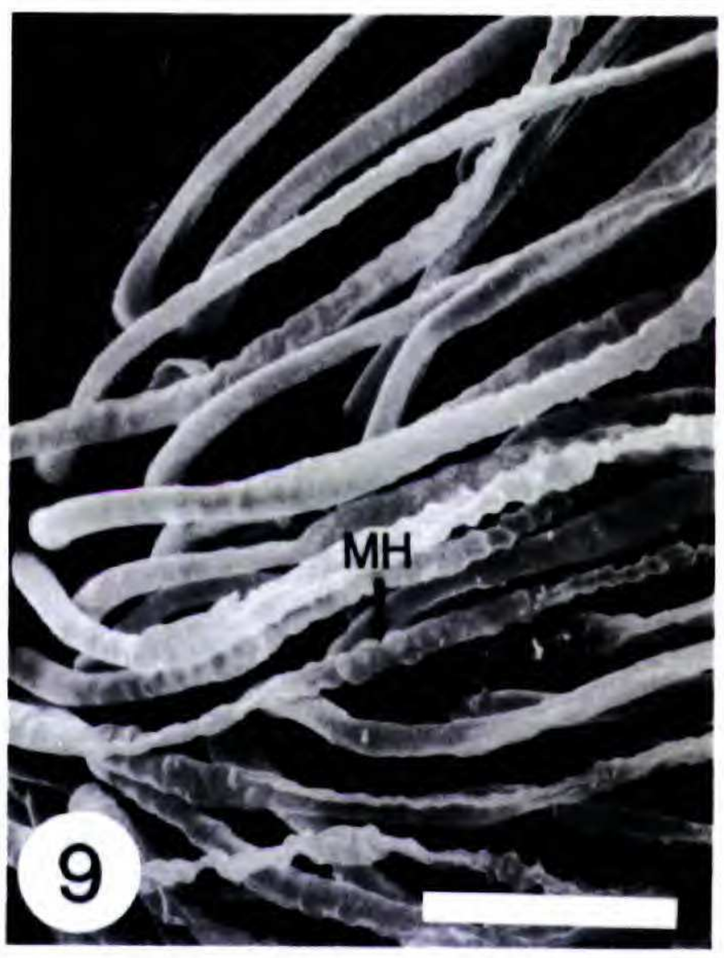
Re-examination of *Leptochloa obtusiflora* suggests some hairs on the lemma are clavate or clavicorniculate (*Mhoro 1868*; *Verdcourt 1101*; both at MO).





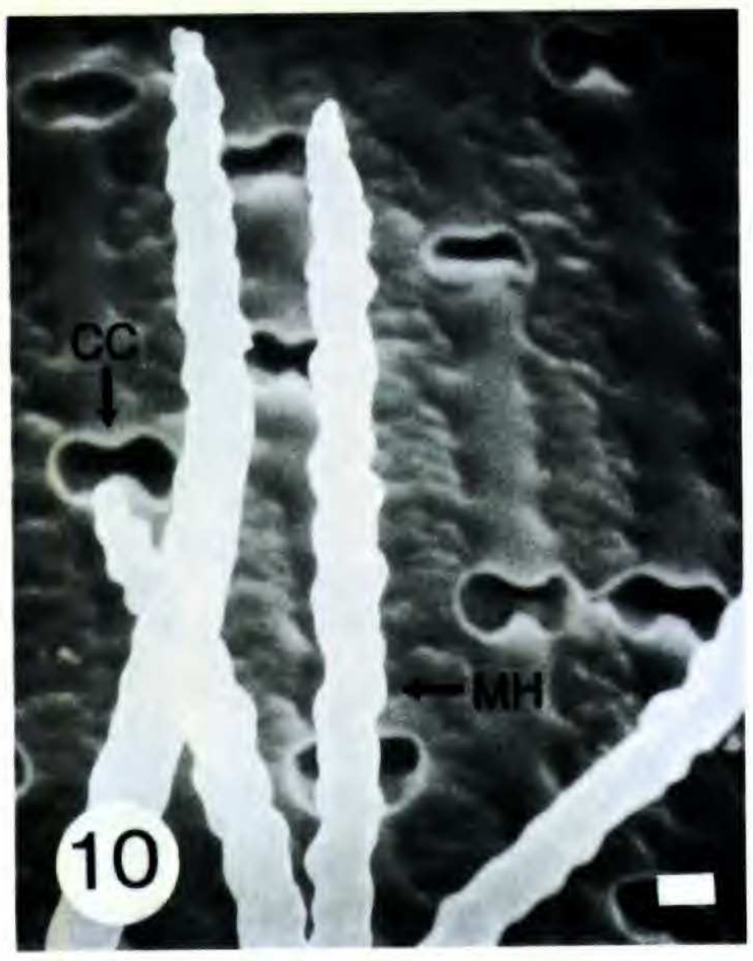


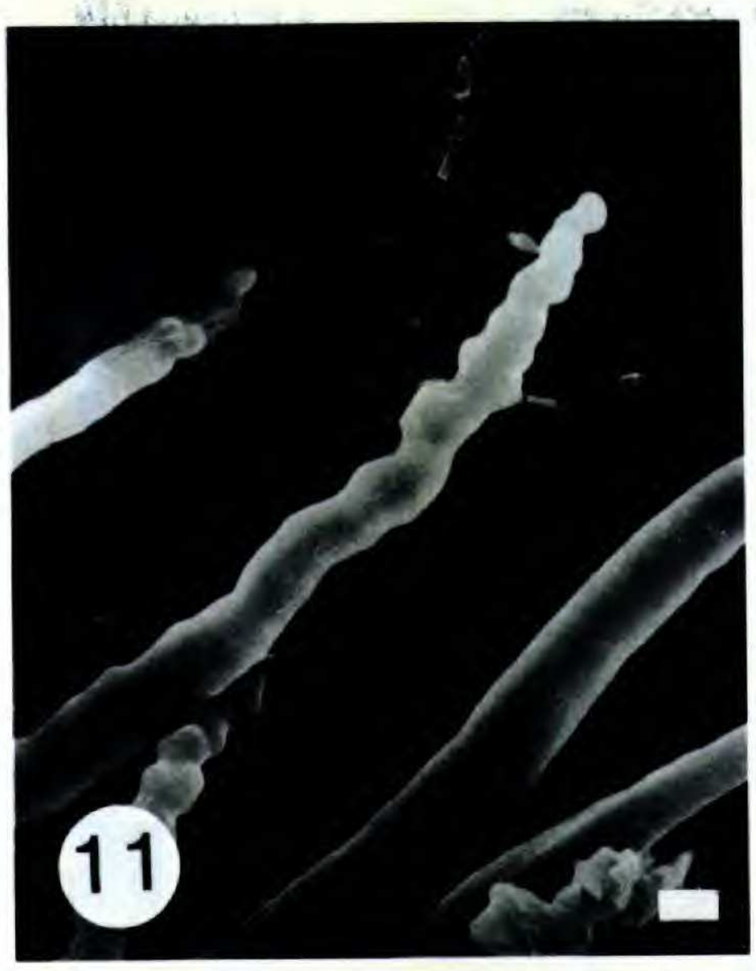


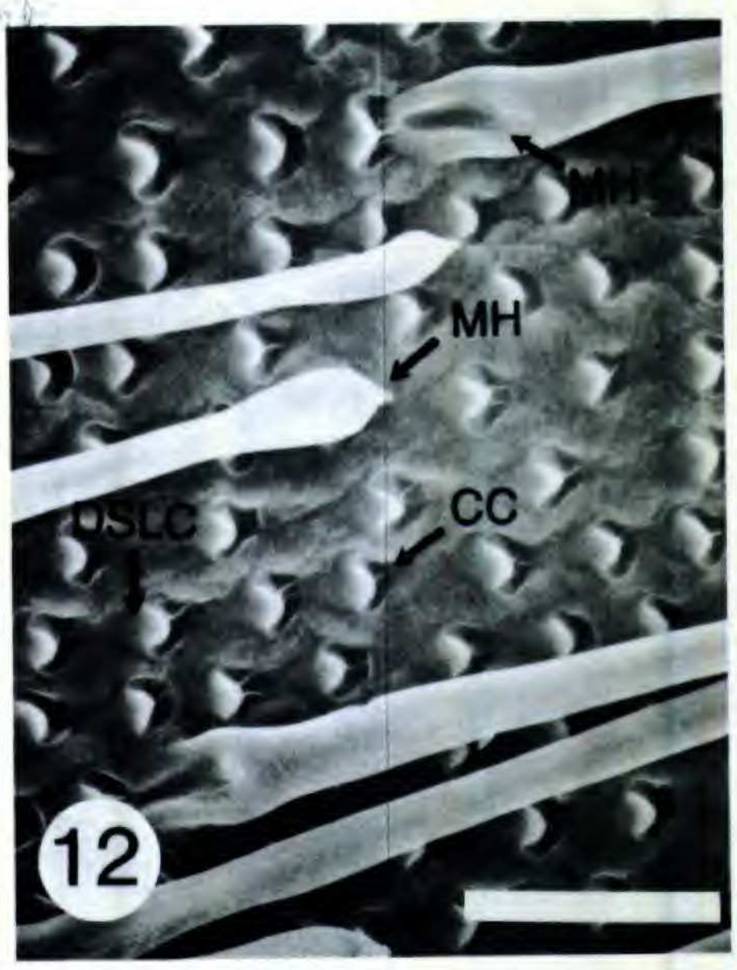


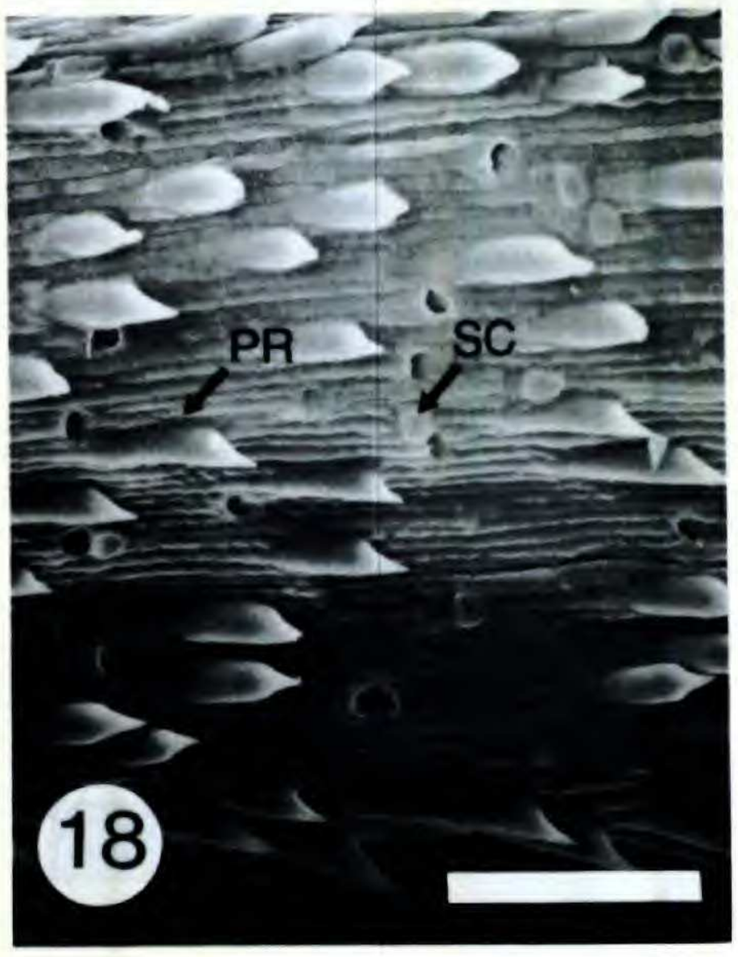
Figures 1–9.[3] —1. *Acracne racemosa.* —2. *Apochiton burttii.* —3. *Bewsia biflora.* —4. *Brachychloa schiemanniana.* —5. *Chloris verticillata*; from left to right, arrows illustrate sequential ontogeny of macrohair. —6. *Cladoraphis cyperoides*; bar = 5 μm. —7. *Cladoraphis spinosa.* —8. *Coelachyrum brevifolium*; note crispate macrohairs. —9. *Coelachyrum poiflorum*, with crispate macrohairs.

[3] Figures 1–72. SEM photomicrographs of lemmas of *Leptochloa* spp. and related genera. Unless indicated otherwise, scale bars equal 50 μm. Abbreviations: AELW = apical extensions of lateral walls of long cells; BM = bicellular microhair; CC = cork cell; DSLC = distally swelling long cell; MH = macrohair; PLC = papillate long cell; PR = prickle; PSC = papillate short cell; SC = silica cell. For details see text.

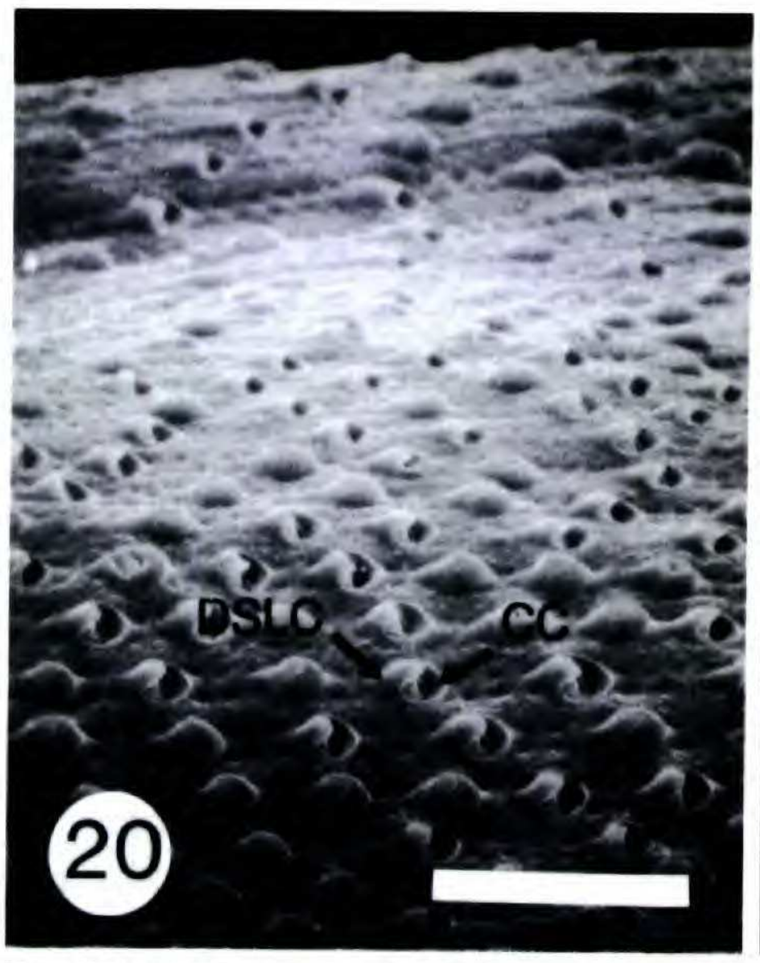


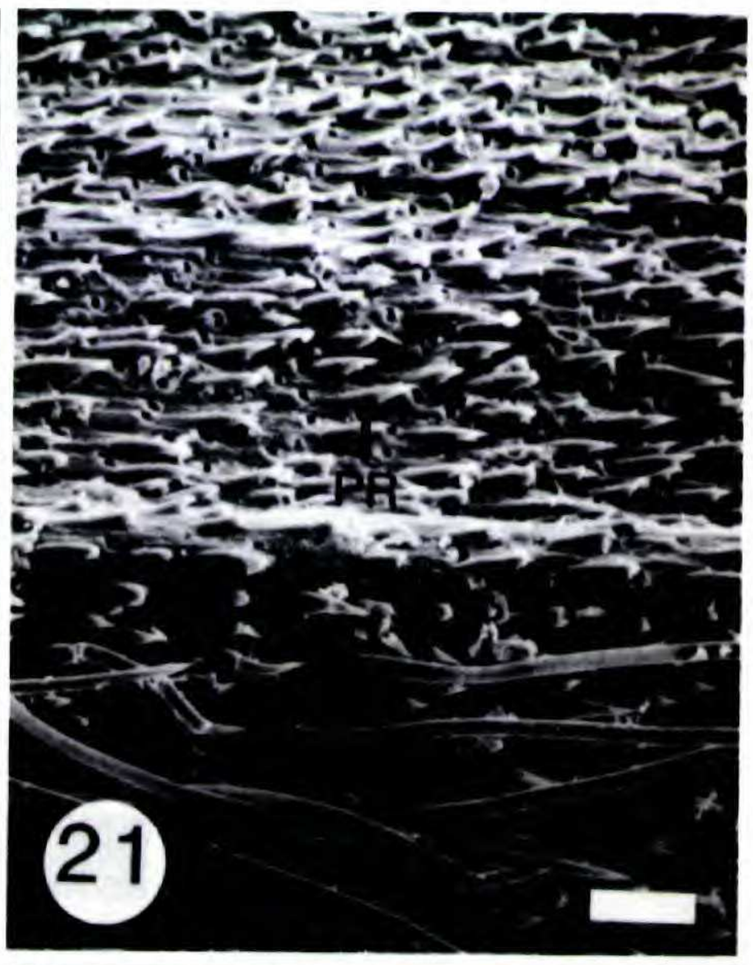


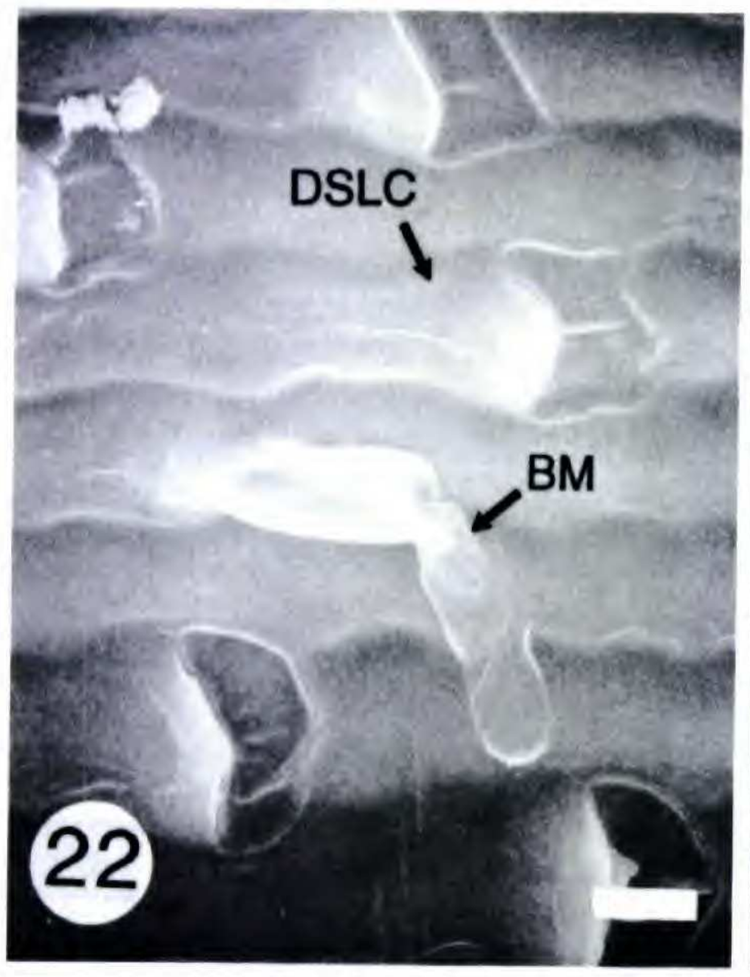


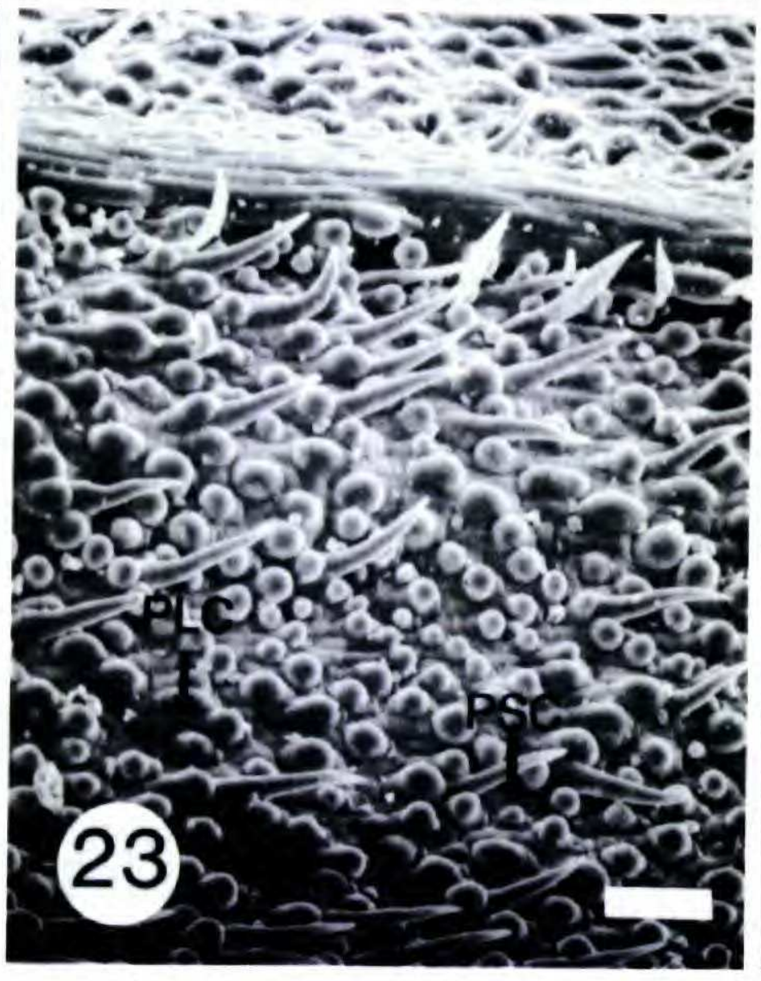


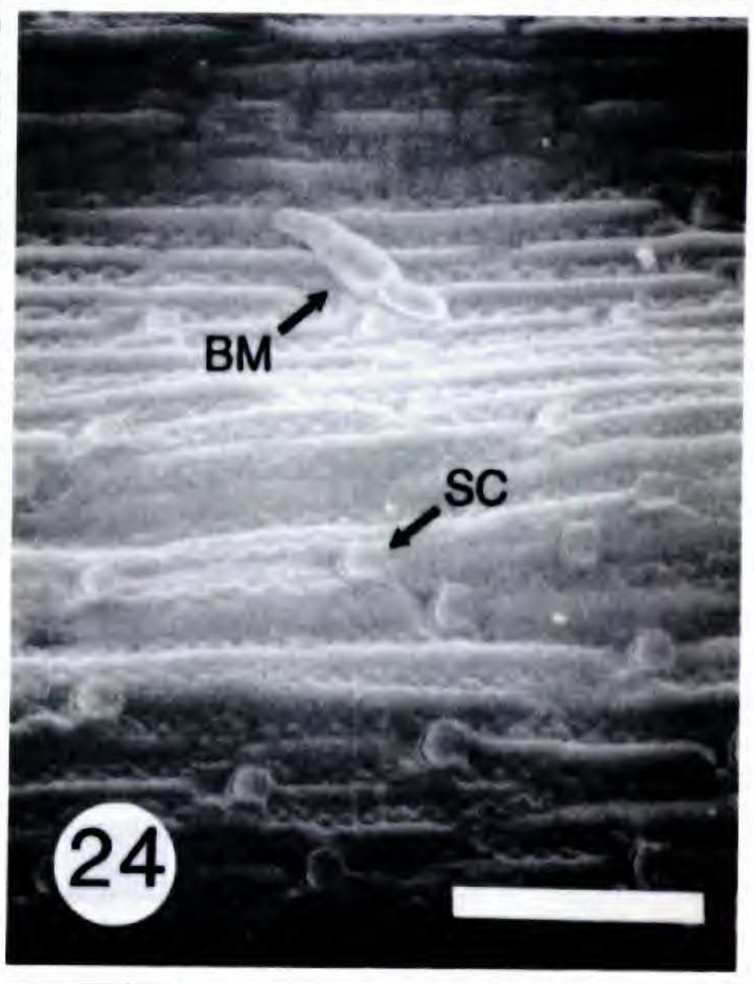
Figures 10–18.[3] —10. *Coelachyrum poiflorum*, note crispate macrohairs and non-swollen long cells; bar = 5 μm (lemmatal apex toward top). —11. *Coelachyrum stoloniferum*, with crispate macrohairs; bar = 5 μm. —12. *Coelachyrum yemenicum*, arrows indicate clavicorniculate apex of macrohairs and basally flattened and conduplicate macrohair bases. —13. *Cynodon nlemfuensis*, showing apiculate tips of macrohairs. —14. *Desmostachya bipinnata*. —15. *Dinebra retroflexa*. —16. *Drake-Brockmania somalensis*. —17. *Ectrosia gulliveri*. —18. *Ectrosia leporina*.

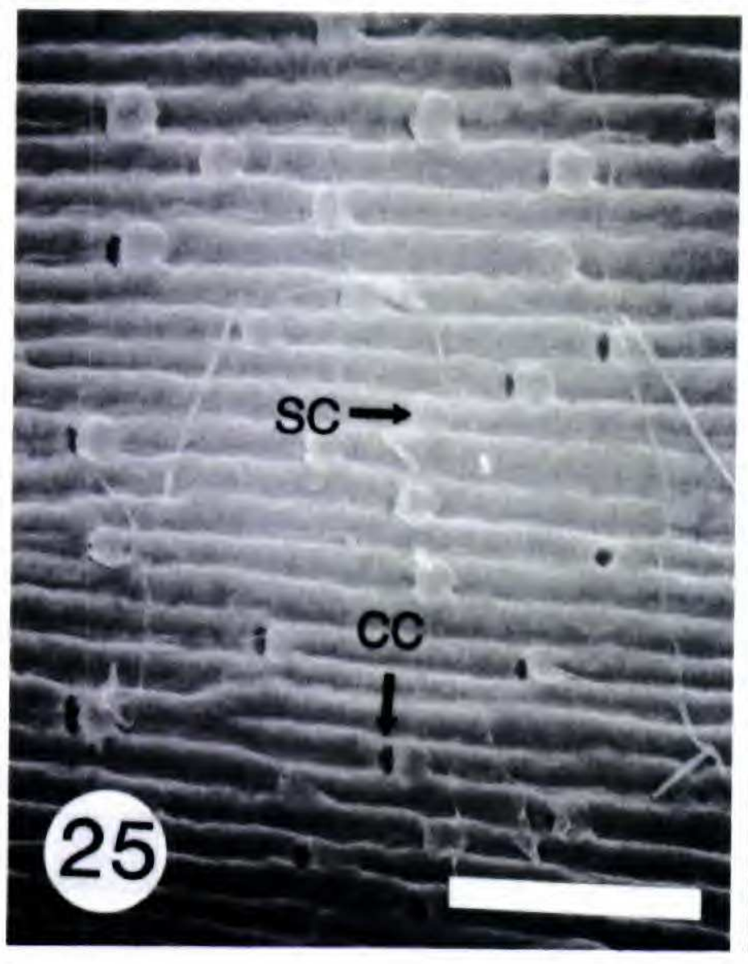


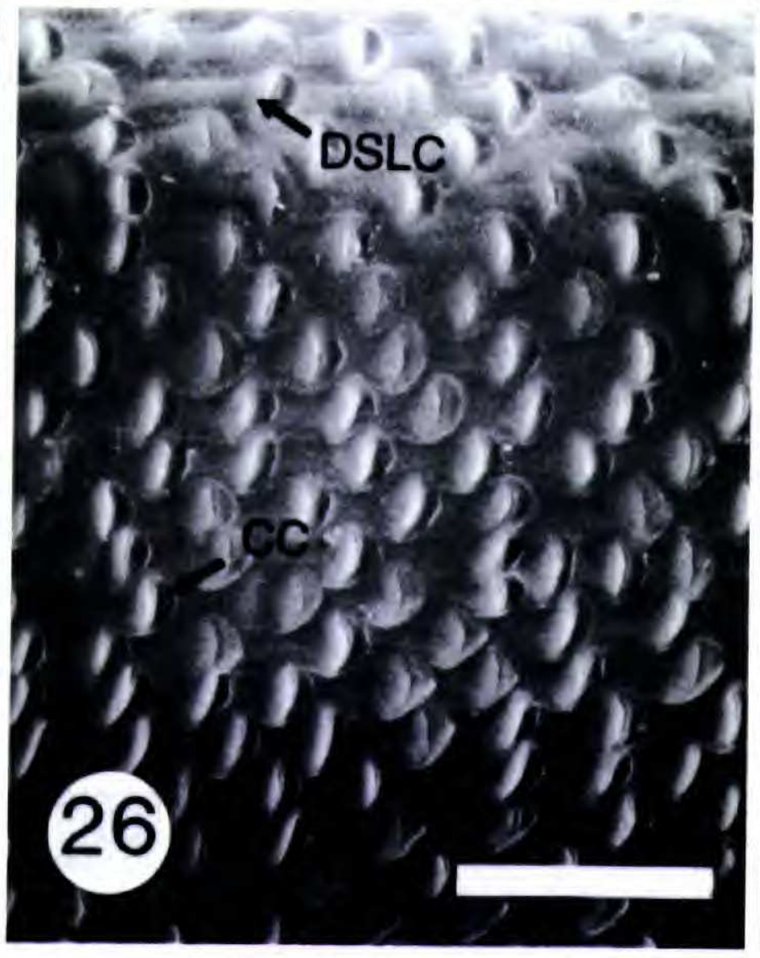


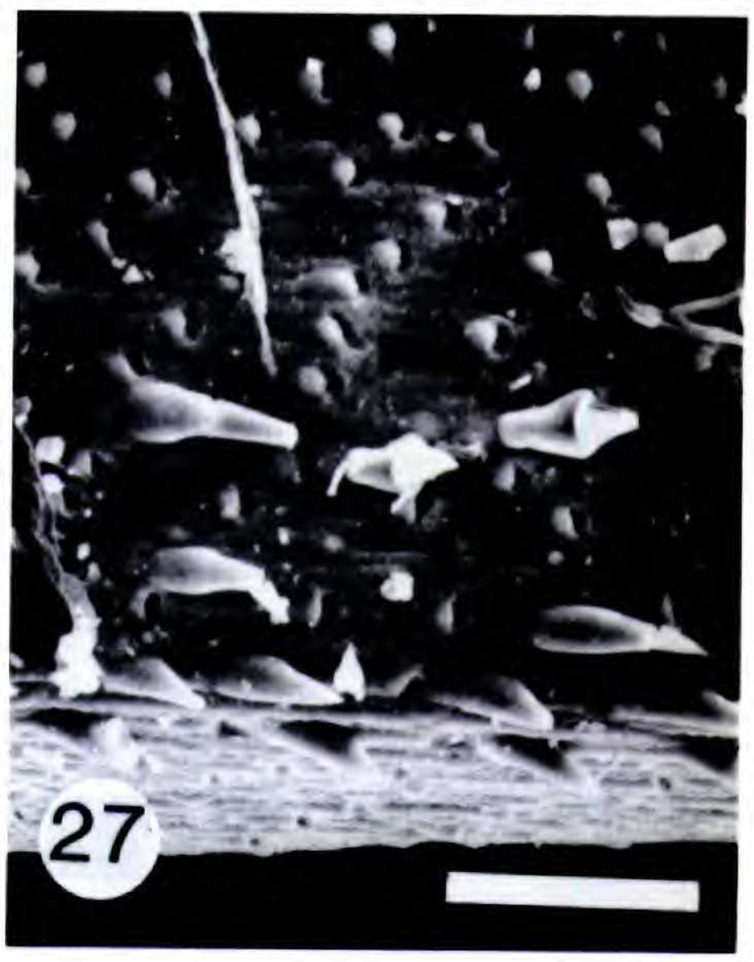




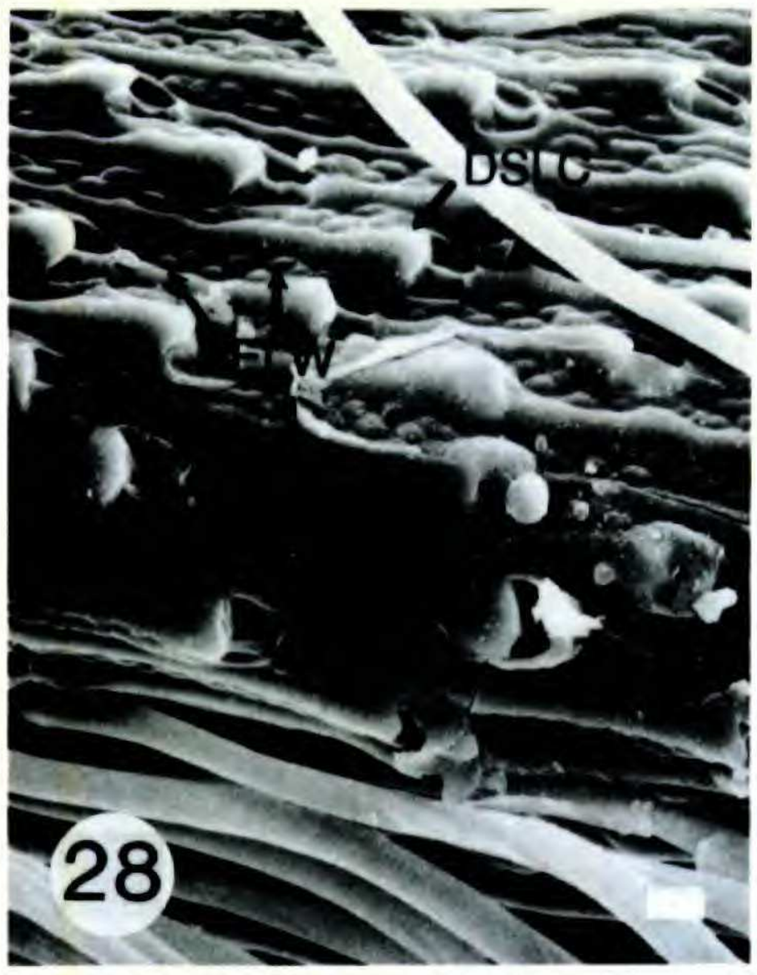


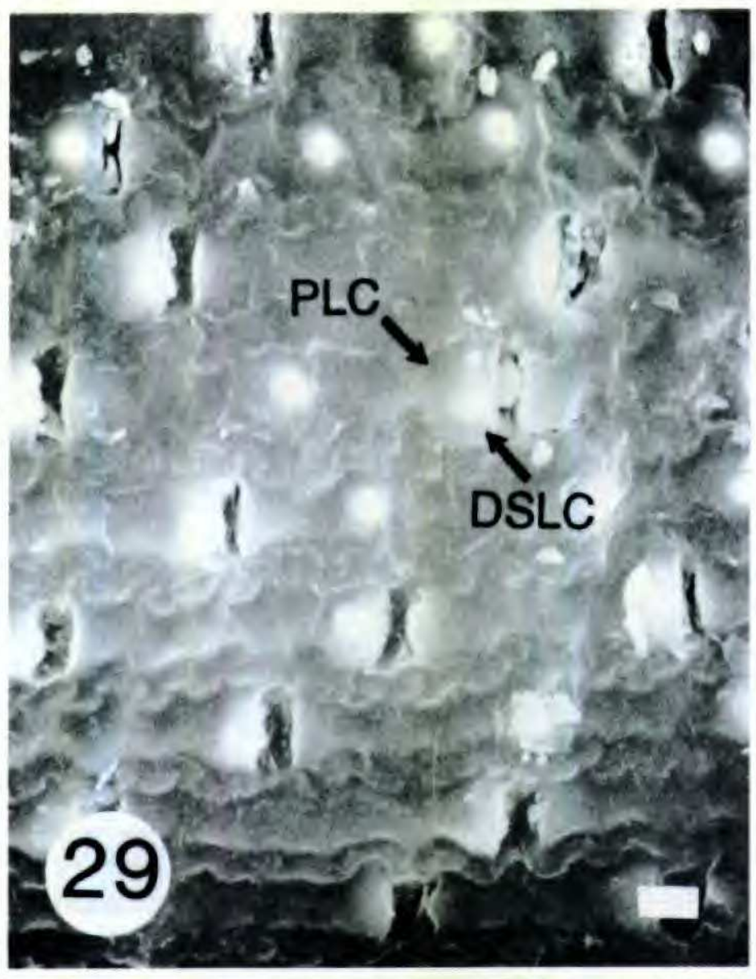


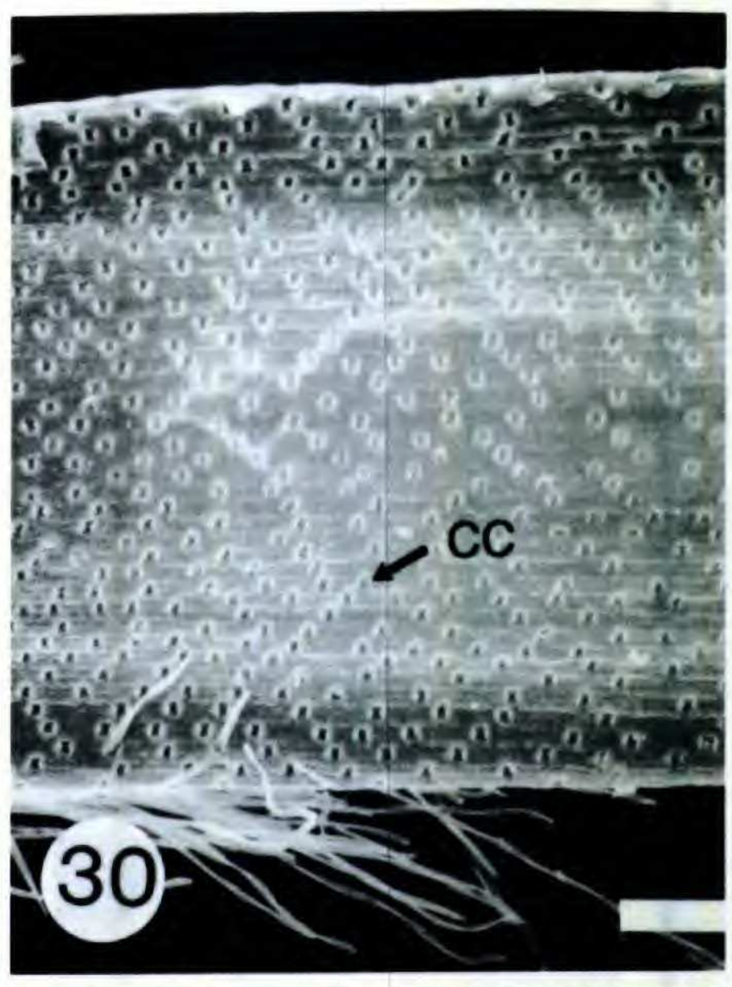


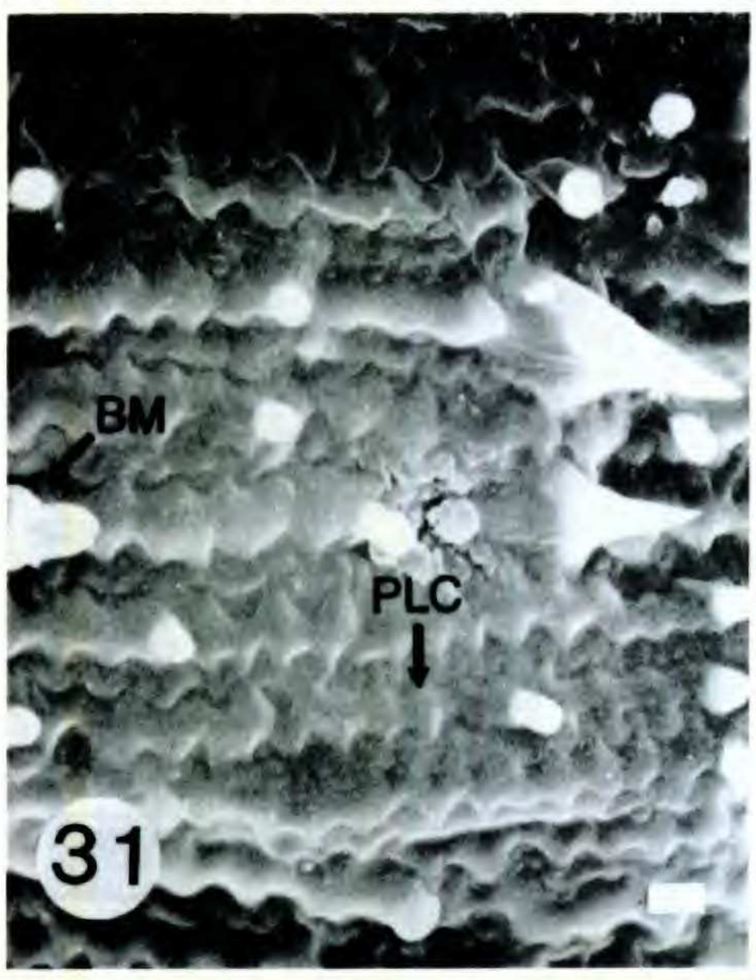


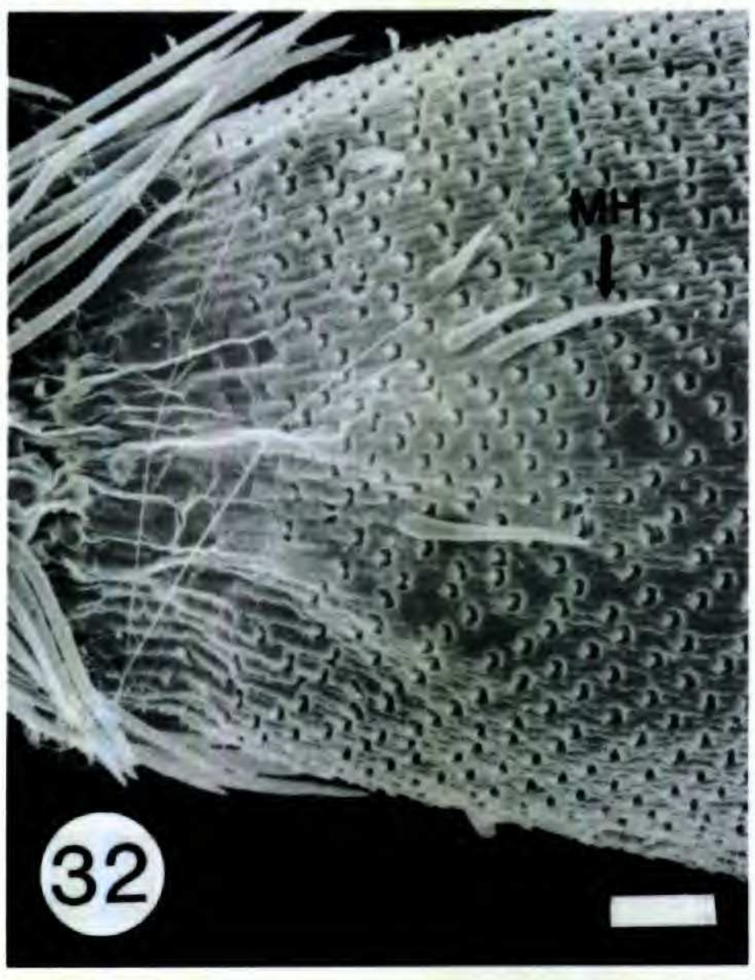
Figures 19–27.[3] —19. *Ectrosiopsis lasioclada.* —20. *Eragrostiella bifaria*; note swollen immature cork cells. —21. *Gouinia virgata*; prickles arising from long cells. —22. *Habrochloa bullockii*, panicoid microhair; bar = 5 μm. —23. *Halopyrum mucronatum.* —24. *Harpachne schimperi.* —25. *Heterachne abortiva*; bar = 5 μm. —26. *Indopoa paupercula*ta; note swollen distal ends of long cells and swollen immature short cells; bar = 5 μm. —27. *Kengia serotina.*

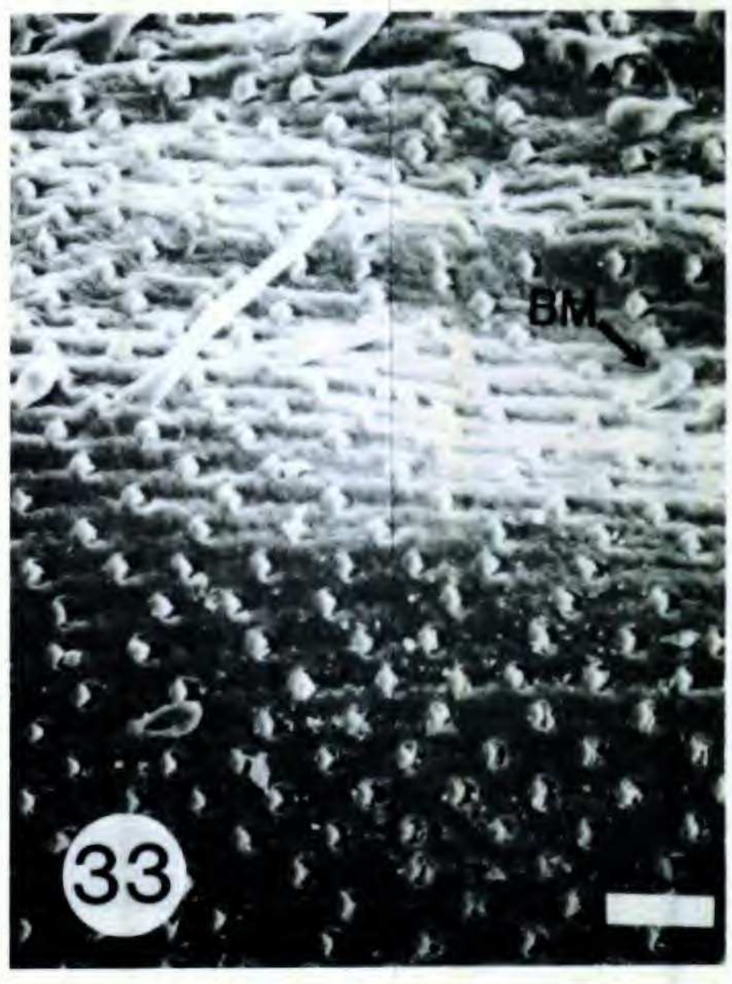


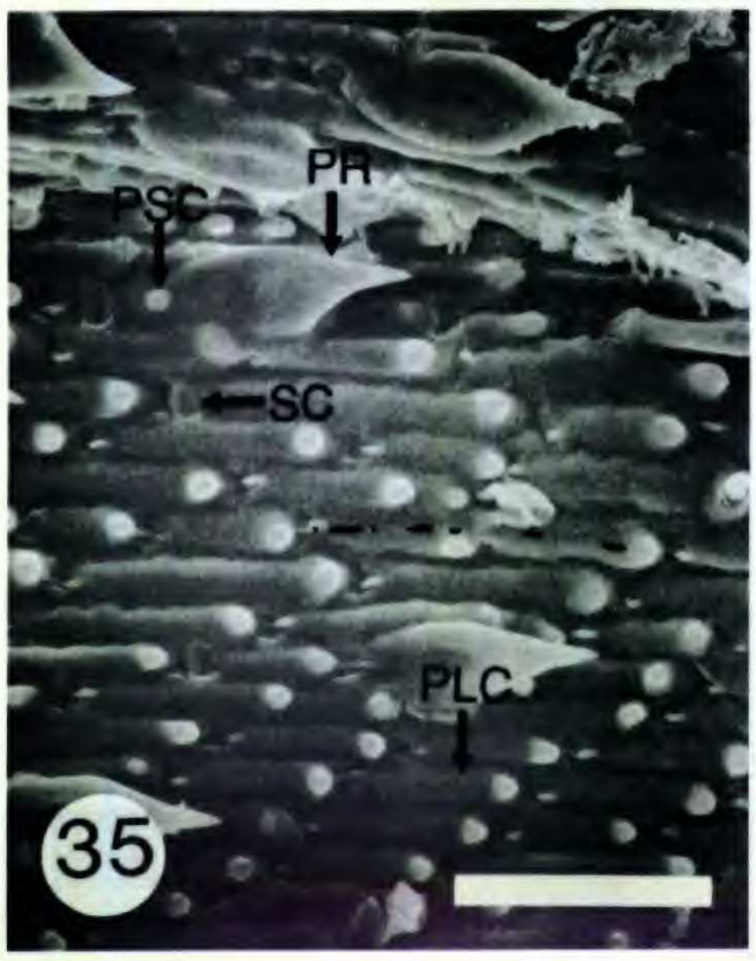




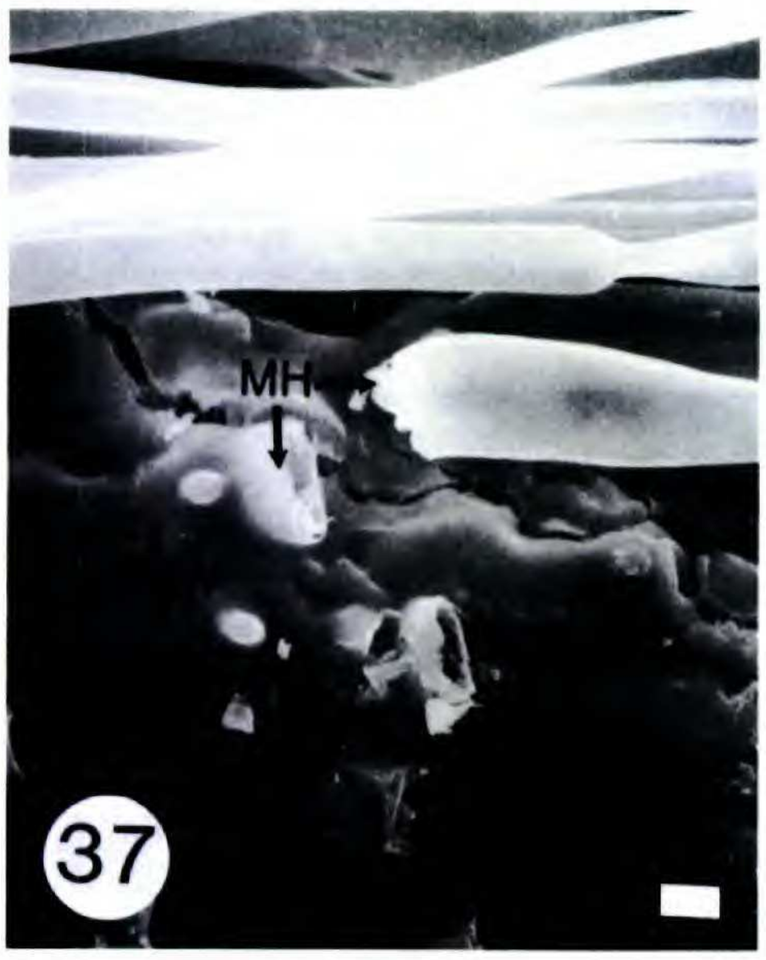


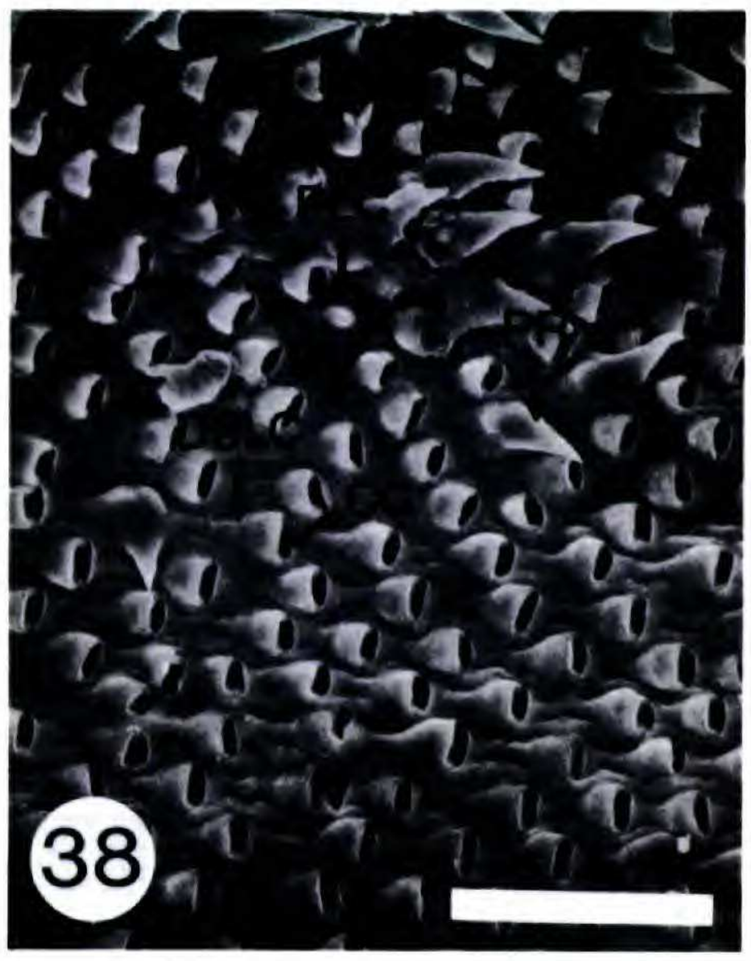


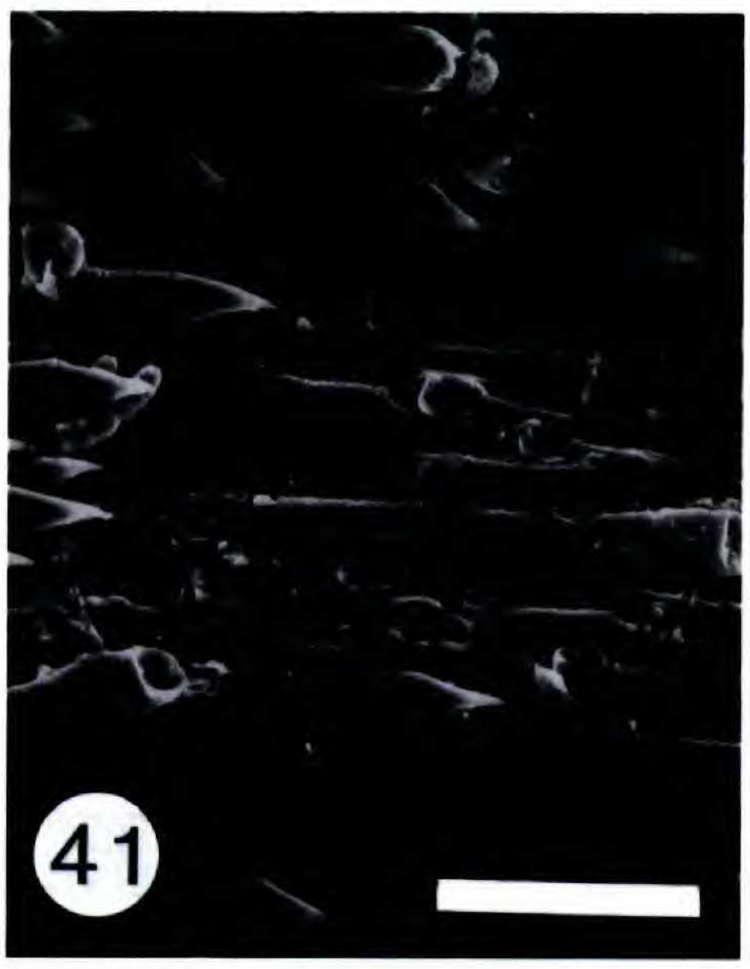


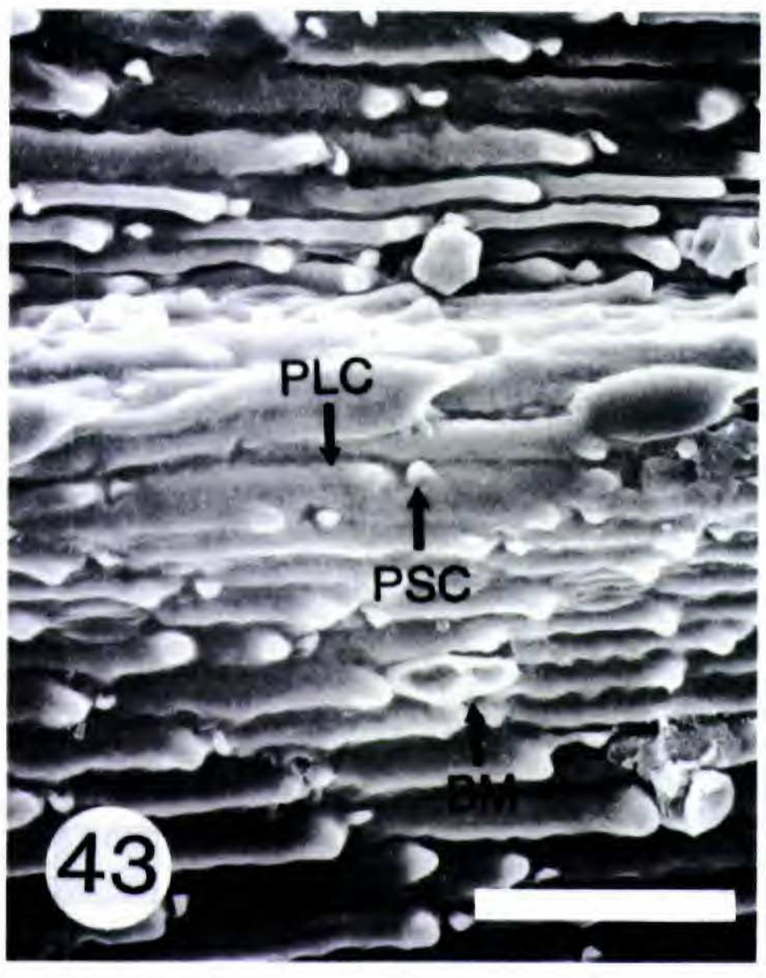


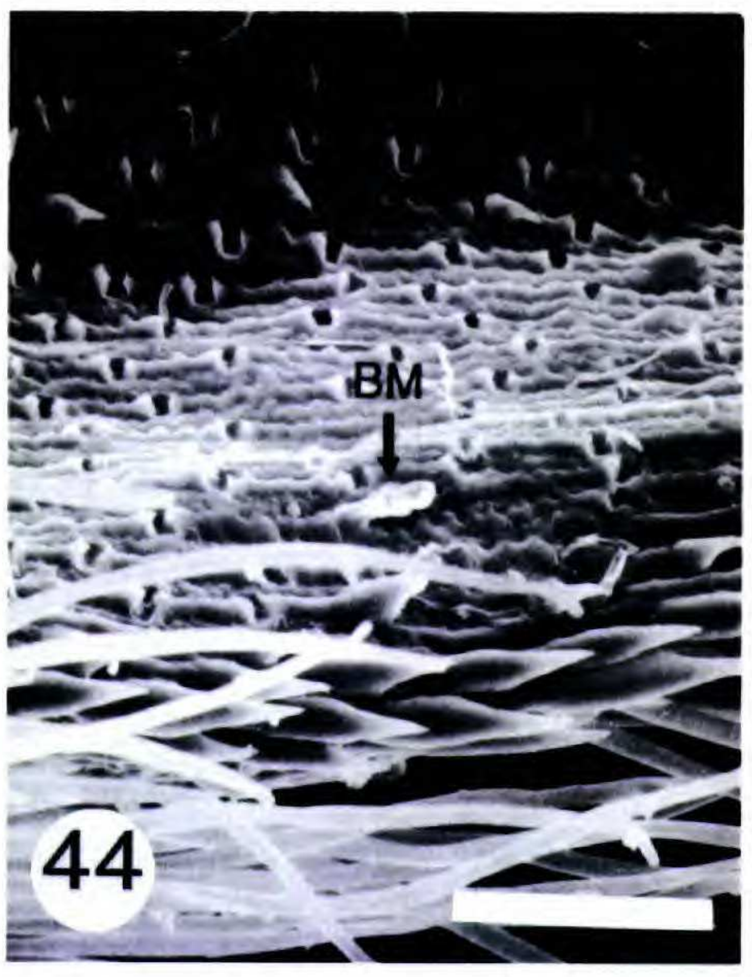
Figures 28–36.[3] —28. *Leptocarydion vulpiastrum*; note apical extensions of lateral walls along long cells; bar = 5 μm. —29. *Leptochloa chinensis*; note papillae occurring on distal swelling of long cell; bar = 5 μm. —30. *Leptochloa ciliolata*. —31. *Leptochloa coerulescens*; chloridoid microhair, papillate long cells, with relatively long papillae; bar = 5 μm. —32. *Leptochloa digitata*. —33. *Leptochloa dubia*. —34. *Diplachne eleusine*, with clavicorniculate macrohairs. —35. *Leptochloa fascicularis*, with a few sporadic silica cells. —36. *Leptochloa fascicularis*; macrohair arising from short cell.



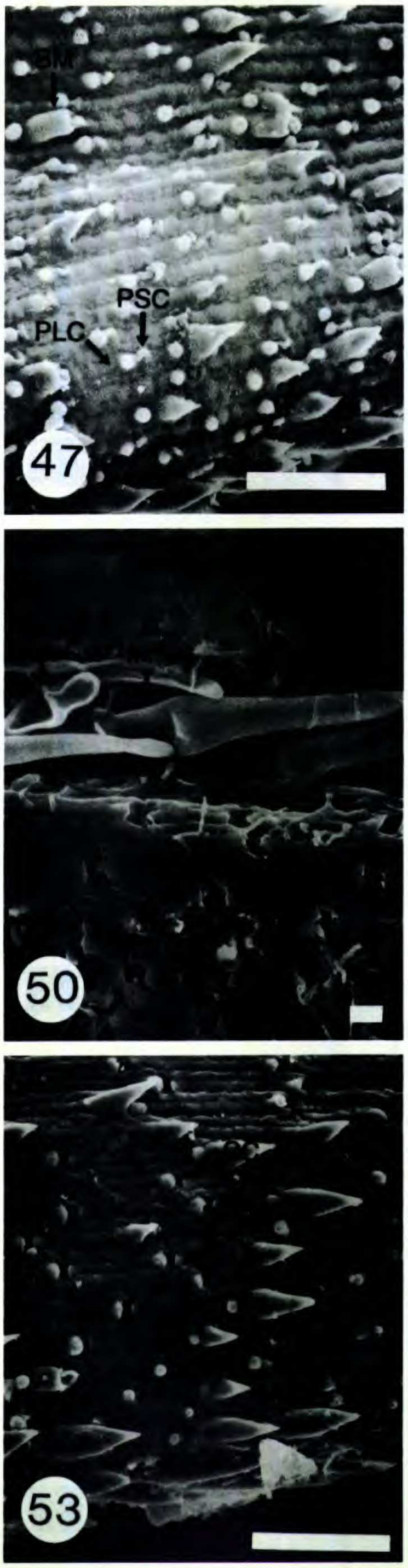




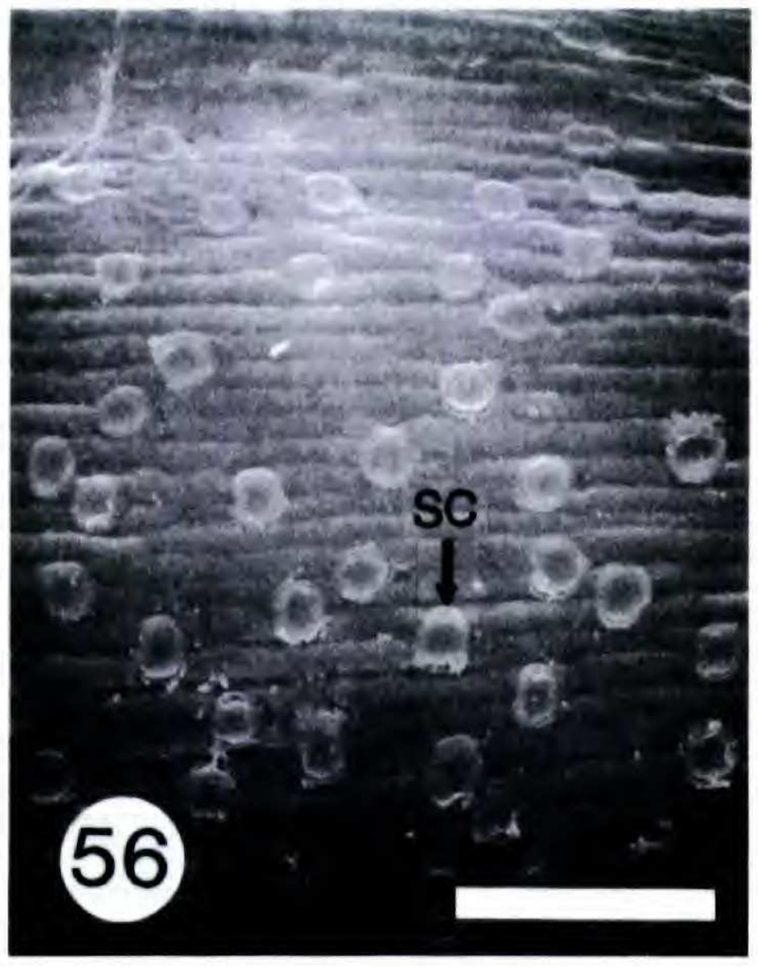


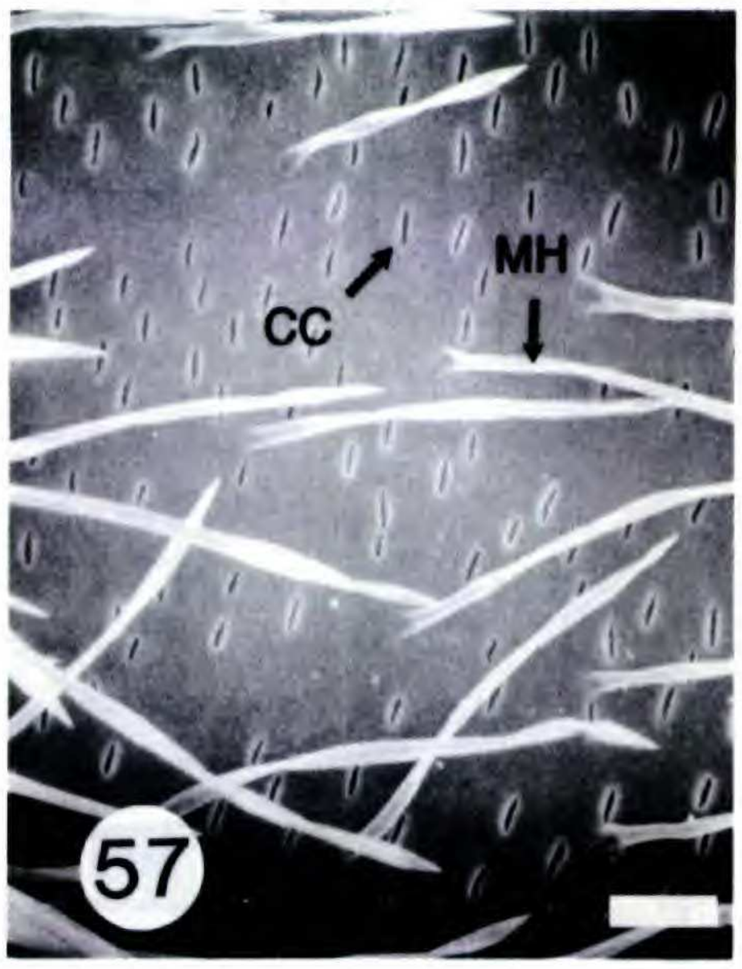


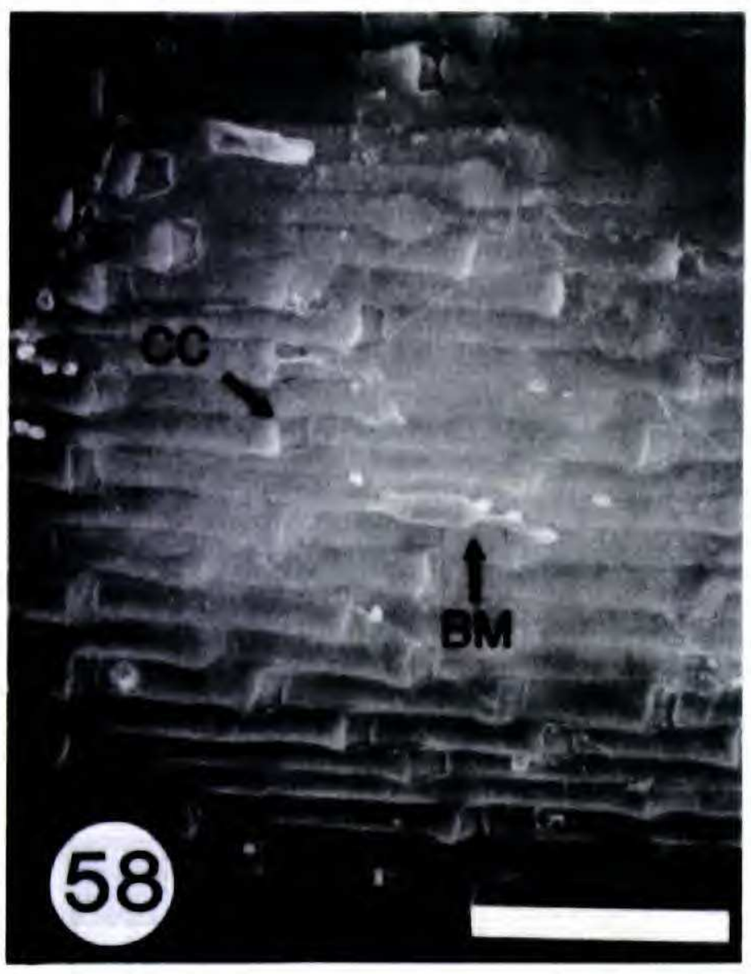
Figures 37–45.[3] —37. *Leptochloa fusca*; bar = 5 μm. —38. *Diplachne gigantea*, with prickles arising from short cells; bar = 5 μm. —39. *Leptochloa ligulata*. —40. *Leptochloa monticola*; note prickles arising from long cells and their conduplicate bases. —41. *Leptochloa monticola* with silica cells. —42. *Leptochloa mucronata*; macrohairs arising from distal end of long cells (lemmatal apex toward top). —43. *Diplachne muelleri*; papillate short and long cells. —44. *Leptochloa nealleyi*; note different prickle sizes. —45. *Leptochloa neesii*, with basally flattened macrohairs arising from short cells; bar = 5 μm.

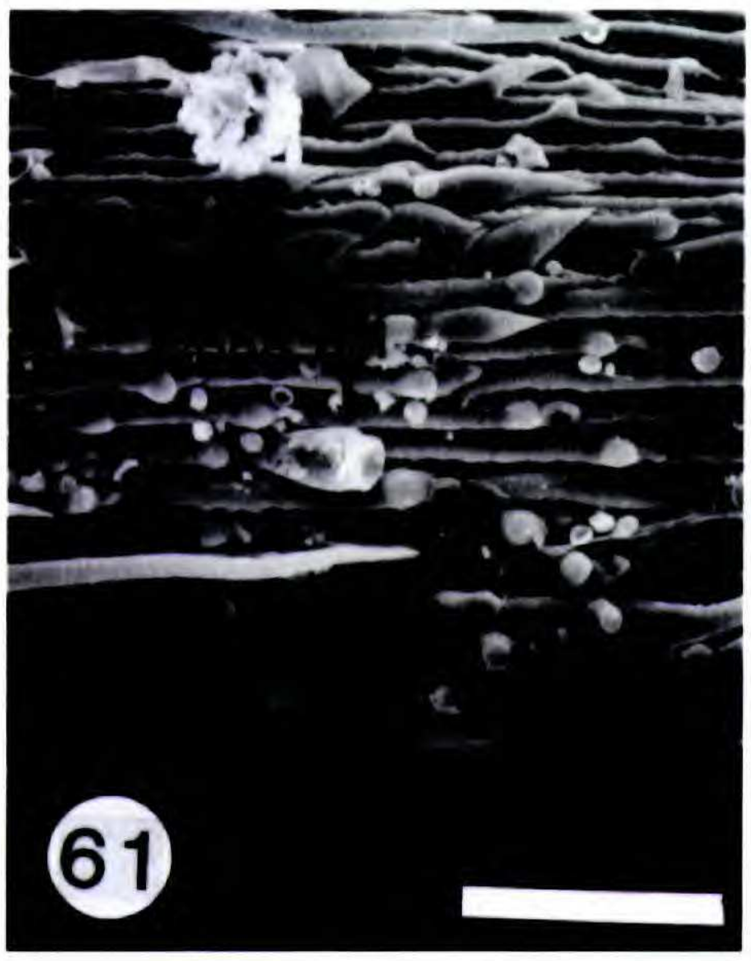


Figures 46–54.[3] —46. *Leptochloa panicea* with intercostal macrohairs. —47. *Leptochloa panicoides*; note thick basal cell of microhair. —48. *Leptochloa rupestris*. —49. *Leptochloa scabra*. —50. *Leptochloa squarrosa*; note basally flattened macrohair; bar = 5 μm. —51. *Leptochloa uniflora*; note atypically shortened long cells. —52. *Leptochloa virgata*, with swollen distal portions of long cells, and cork cells with collapsing outer walls. —53. *Leptochloa viscida*; note thick basal cell of microhair. —54. *Lintonia nutans*, with prickles arising at base of dorsal awn.

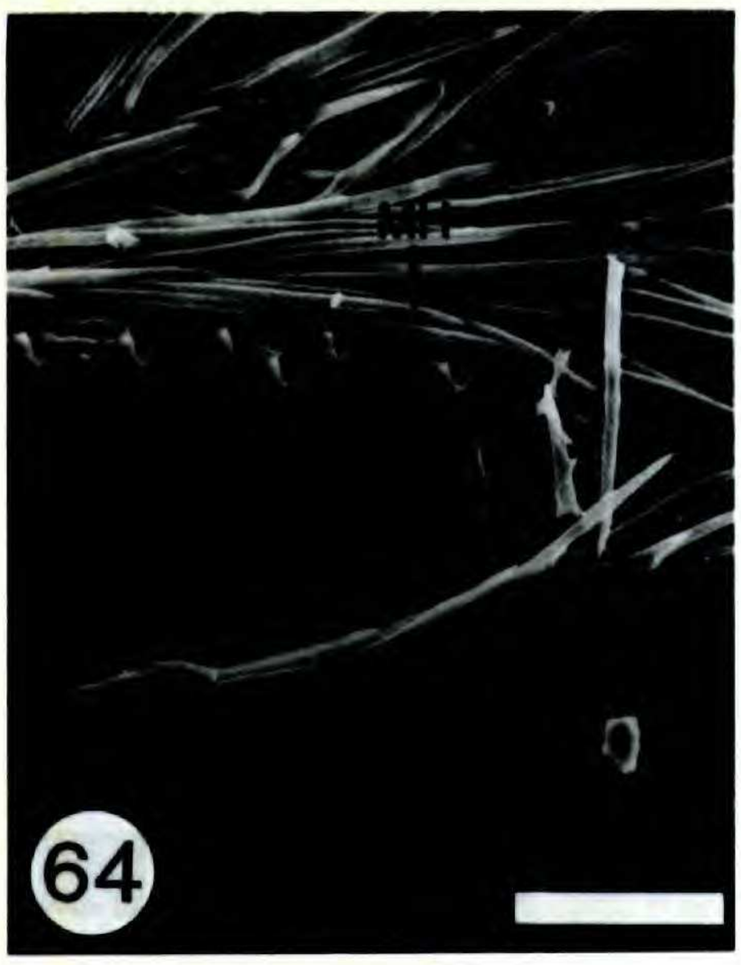


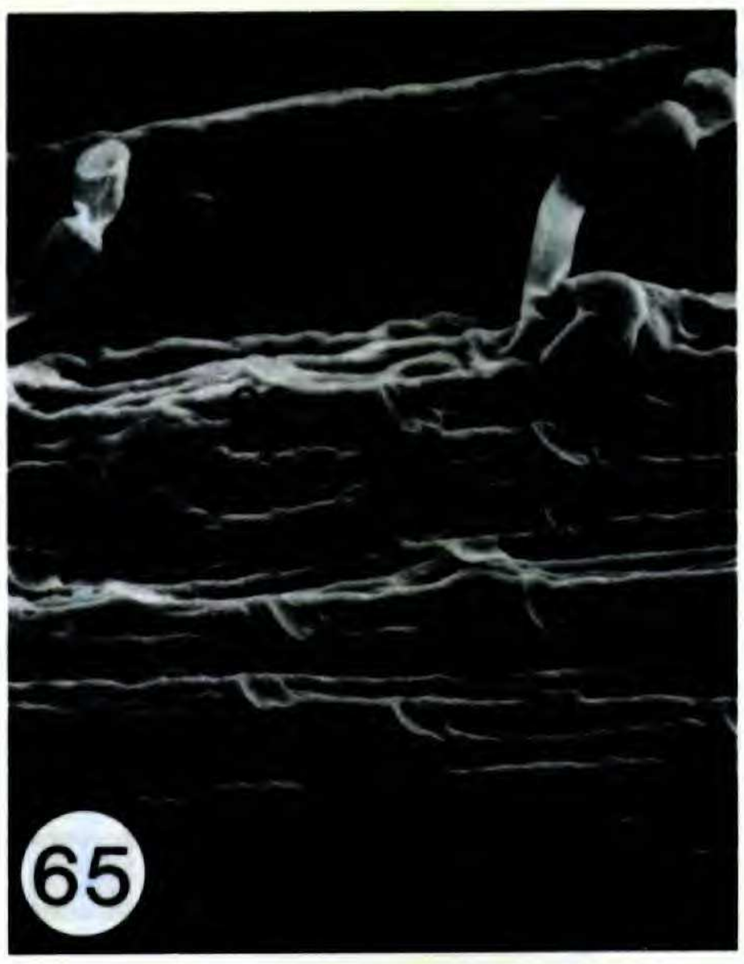


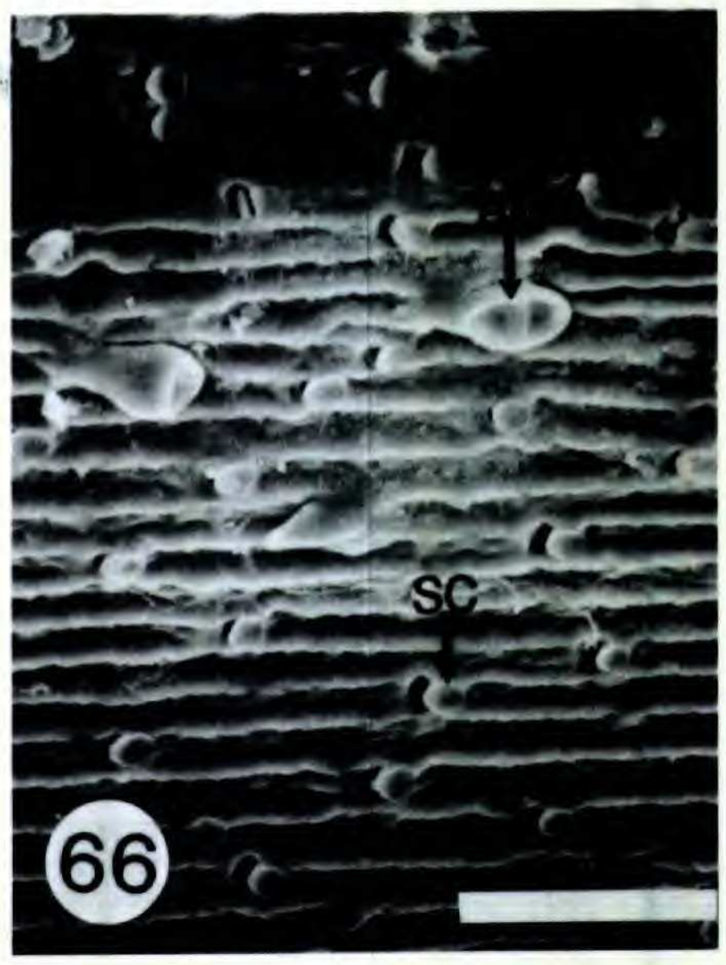


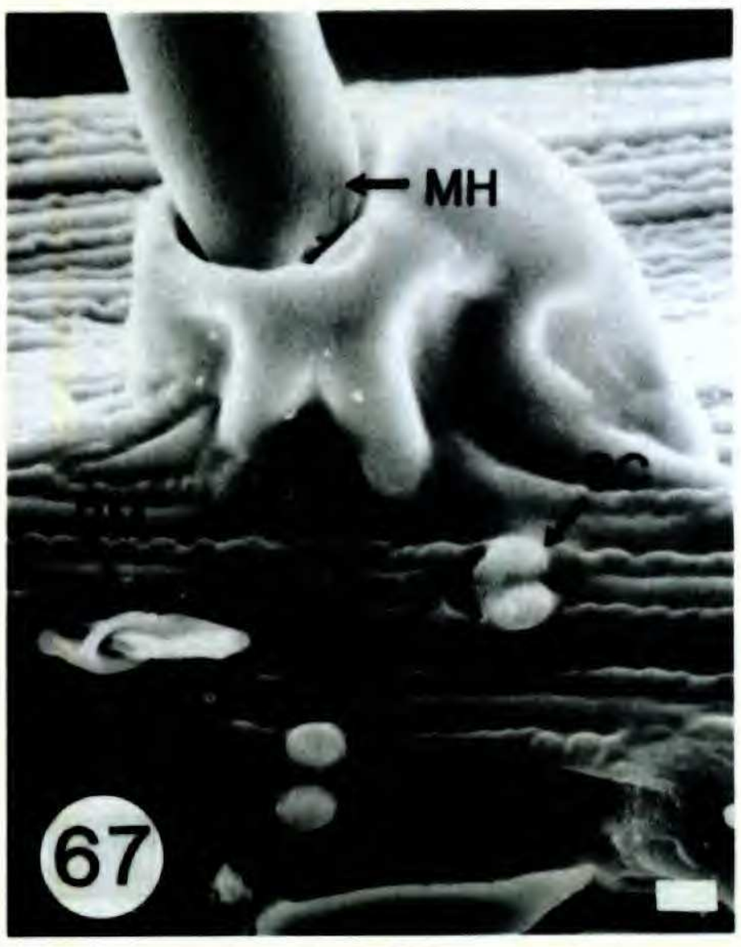


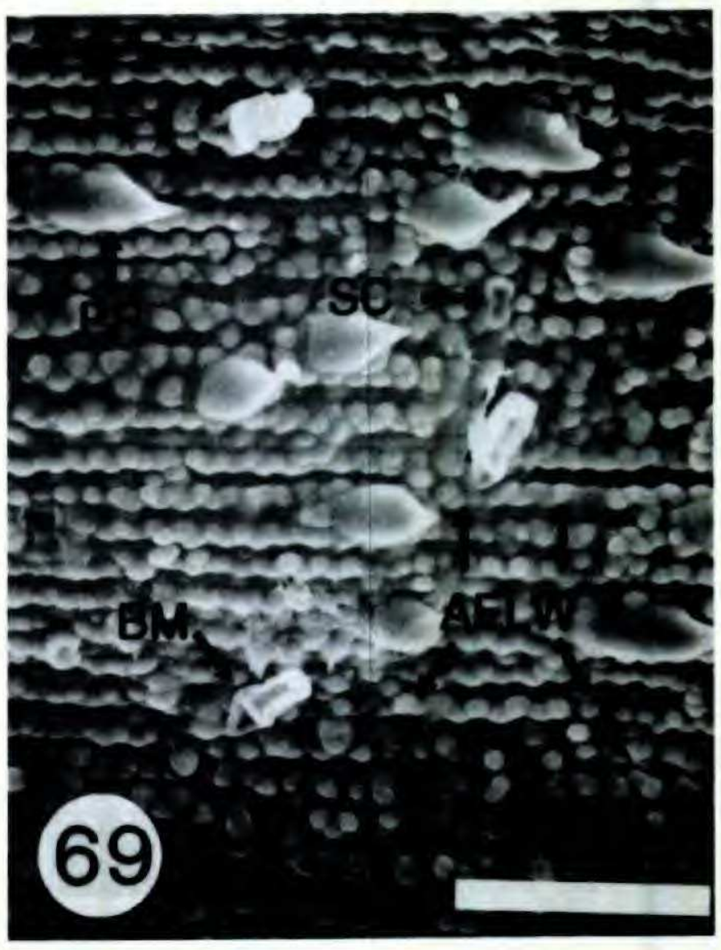
Figures 55–63.[3] —55. *Lophacme digitata*. —56. *Myriostachya wightiana*. —57. *Neesiochloa barbata*. —58. *Neyraudia reynauldiana* with panicoid microhair. —59. *Ochthochloa compressa*, showing hollow, basally severed macrohair; bar = 5 μm. —60. *Odyssea mucronata*; bar = 5 μm. —61. *Orinus thoroldii*. —62. *Oropetium aristatum*. —63. *Pogonarthria fleckii*; prickles arising from long cells and short cells.











Figures 64–72.[3] —64. *Pogoneura biflora*. —65. *Psammagrostis wiseana*; note enneapogonoid microhairs and swellings distal to the base of the microhair. —66. *Psilolemma jaegeri*. —67. *Richardsiella eruciformis* with papillate base of macrohair; bar = 5 μm. —68. *Sclerodactylon macrostachyum*. —69. *Steirachne barbata*; note apical extensions of lateral walls of long cells. —70. *Trichoneura grandiglumis*; note macrohairs with swollen bases (above) and macrohairs arising from the proximal end of long cells (below). —71. *Triraphis andropogonoides*. —72. *Viguierella madagascarensis*; bar = 5 μm.